THE BOTANICAL RESULTS OF THE U.S. COMMISSION OF INQUIRY TO SANTO DOMINGO IN 1871

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In the Gray Herbarium there is a small collection of specimens which were prepared by Charles Wright, C. C. Parry, and H. Brummel during a difficult period of United States-Latin American relations nearly a century ago. The specimens bear little information beyond the name, and yet approximately forty of these are "new species" which were never published. Supporting this collection is a 130-page handwritten manuscript entitled "Flora Domingensis" and attributed to Asa Gray and Charles Wright. This, too, was never published, although with a revision of only a few pages, the manuscript, with Latin descriptions of the new species, geographical localities, and dates would have been ready for the printer. One wonders why the manuscript prepared with such care was not published; why the specimens with incomplete labels and often conflicting numbers were so haphazardly distributed to herbaria; why two such competent collectors as Wright and Parry left so little record of their expedition together; and who was the botanist H. Brummel, who is today unknown among the collectors of West Indian vegetation.

Asa Gray, in a necrology of Charles Wright (Am. Jour. Sci. **31**: 17. 1886) states, "The small collection made in this, his last distant botanizing, was not of much account." Parry's biographers refer to the Santo Domingo trip as a not very successful expedition, and Urban states (Symb. Ant. **3**: 143. 1902) that the botanical results of this expedition made during an unfavorable part of the year and on a hasty trip were not outstanding. These comments seem inappropriate when applied to an expedition in an area which later yielded hundreds of new species to Eric Ekman; to a collection of nearly 700 numbers; and to a manuscript which might have been one of Charles Wright's outstanding publications.

From many sources, particularly the letters of Wright, Gray, Torrey, and Oliver in the historical files of the Gray Herbarium, it has been possible to piece together notes and comments to supply this documentation of the botanical results of the U.S. Commission of Inquiry. I am grateful to Dr. Reed Rollins, director of the Gray Herbarium, for permission to publish this report on an historical document in the Gray Herbarium files;

HISTORY OF THE COMMISSION OF INQUIRY

The island of Hispaniola, comprising the countries of Haiti and Santo Domingo (now the Dominican Republic), lies in an important position in the Caribbean. In the 19th century, at the time of the Commission of Inquiry, it was subjected to the interests of European countries and was torn by internal strife. There was a desire on the part of some groups in Hispaniola and of many parties in the United States for the annexation of the country to the United States. Negotiations for annexation had been carried on during the administration of President Andrew Johnson (1865–1869) to bring about at least the acquisition of Samaná Bay to serve as a strategic naval station — a guard post for the Mona Channel, the gate to the Caribbean sea and the Isthmus of Panama. Soon after the inauguration of President Grant in 1869, the question of annexation was revived. The government of Santo Domingo sent an envoy to President Grant to solicit his consideration in the matter of Dominican affiliation with the United States. To ascertain the true state of affairs on the island Grant dispatched General Orville Babcock as a confidential agent to Santo Domingo. From Babcock's report Grant became convinced, first, that what had seemed a fabulous account of agricultural and mineral resources was true; second, that it would be advantageous to obtain Santo Domingo because of its value as a mercantile and naval station; third, that the people of Santo Domingo truly were desirous of their country's annexation to the United States; and finally, that by annexing Santo Domingo it would be possible to strengthen the Monroe Doctrine, since Santo Domingo thus would avoid domination by European powers. Working from these premises, Grant set about to have passed a treaty for the annexation.

Grant's efforts met with bitter opposition from European traders who wished to monopolize the Dominican trade, from the aggressive Negro party in Hispaniola which hoped to gain control over the established Dominican government, as well as the entire island, and from some American groups whose spokesman, Charles Sumner, led the fight against annexation. When Babcock's reports were challenged, Grant established

through an act of the U.S. Senate a new party of investigation. The Commission was headed by Dr. Samuel Howe, a noted philanthropist, Benjamin Wade, a former senator, and Andrew White, the president of Cornell University. These three, with their supporting assistants, secretaries and scientists, called themselves the U.S. Commission of Inquiry to Santo Domingo. They visited Santo Domingo during the latter part of January through early March, 1871, and submitted their report, which was published as the Executive Document 9, 42nd Congress, 1st Session, 1871. The goal of the Commission was to survey the natural resources; the nature of the health, education, and government of the people; the nature of foreign claims to the area; and the attitude of the people to annexation. These goals were met fully. Although the report for the most part supported the idea of annexation, the proposal itself was defeated in the U.S. Senate. In due time even the lease on Samaná Bay was abandoned, and some years later a naval base was established in Guantanamo Bay, Cuba, as an adequate substitute.

ACTIVITIES OF THE COMMISSION

The Commission of Inquiry consisted of twenty-two official representatives traveling at government expense and ten representatives of the press who were given transportation. The scientists, in the order and with the title given in the official report, were: Prof. W. P. Blake, geologist and mineralogist; Prof. C. C. Parry, botanist; Dr. W. Newcomb, naturalist; A. R. Marvine, assistant geologist and mineralogist; E. Waller, assistant mineralogist and chemist; J. S. Adam, assistant mineralogist and chemist; Prof. H. A. Ward, zoologist and paleontologist; C. Wright, botanist; and H. Brummel, botanist. There is no information on how these men were selected, but it is apparent from the titles throughout the report that Parry was considered to be the principal botanist and that Wright and Brummel were considered as aides. At the time of the expedition, Parry was not a professor but was officially botanist for the U.S. Department of Agriculture, having been appointed to that post in 1868. Brummel apparently was an employee of the Department of Agriculture, and nothing can be found on his professional career either prior to or after the trip. Charles Wright, well known as a botanical collector, had completed his last trip to Cuba in the summer of 1867 and was operating a farm in Wethersfield, Connecticut, during the summers and working as an assistant to Asa Gray, at the Gray Herbarium in Cambridge, Massachusetts, in the winter. Both Parry and Wright were well known to Gray, and it is possible that he suggested Wright for the trip. Wright was 60 years old and in poor health at the time of the expedition, and one wonders what inducement led him to join the Commission.

The large number of reporters accompanying the Commission indicates the delicate nature of the investigations and the interest of the newspapers and the public in their findings. There is even a suggestion of intrigue in the official report of the trip. The assistant to the confidential secretary

of the Commission was discharged and sent back to New York, with the note being made in the report that this man had misrepresented himself and was, in fact, an assistant editor of an important New York newspaper. Although the reporters were supposed to be observers, the Commission delegated several of them to make special trips to gather information, with power to conduct interviews on behalf of the Commission. Letters from these reporters were published in many papers in the United States while the expedition was in the field. Feeling about the trip and the principle of annexation was high in the United States. John Torrey and Asa Gray, both to be involved in an aftermath of the Commission's trip, expressed opinions against the principle of annexation of Santo Domingo.

The Commission left New York on January 17, 1871, aboard the U.S. Steam Frigate "Tennessee" heading for Santo Domingo City. Supplies of coal ran low en route, and, on January 24, the "Tennessee" stopped in Samaná Bay, where it was joined by the cutter "Nantasket." Coal had been reported along the shores of Samaná Bay, but on investigation this proved to be a low-grade lignite. While at anchor in Samaná Bay, the Commission and its scientists were divided into parties with different assignments. One party investigated the shoreline and the anchorage of the bay, while another went to the interior of the Samaná peninsula. A third party was sent overland to Santo Domingo City with a message for the secretary of foreign affairs to announce the impending arrival of the "Tennessee" and the Commission in the capital. Still another group was sent overland to the capital to investigate the resources en route, and a last party was sent to Puerto Plata by the north coast. The "Tennessee" remained in Samaná Bay until January 29th, when it departed for Santo Domingo City, arriving there on the 31st.

On January 26th, the Commission resolved "that the botanists attached to the expedition be requested to examine and report to the Commission regarding the trees, plants, roots, and grains and their vegetable products of that part of the island adjacent to the Bay of Samana, especially with regard to such trees and plants as may be of commercial value, or in any way decidedly useful to man." According to the published report, Parry was the botanist to make this trip in a party headed by the geologist Blake. Contrary to the report, Wright's letters to Asa Gray (January 31, 1871; February 5, 1871) indicate that he also made this trip. The party left the anchorage off Samaná on January 26th and proceeded to Punta Corozos, Punta Mangle, Punta Grigri, Los Róbalos, Cabeza de Toro, and Santa Capuza, where they spent the night. On January 27th the party visited Punta Gorda, where they investigated the reported coal seam, and then proceeded to Canitas, the mouth of the Yuna river, and back to Cabeza de Toro for a night anchorage. The following day, January 28th, the Blake party visited Punta Corozos and returned to the "Tennessee" off Samaná. Parry wrote the official report of this trip entitled "Report on the botanical features, agricultural products and timber growth of the peninsula of Samana." In it he described the cultivated crops, grasses, fibers, fruits, palms and timber trees. He also stated, "The short interval allowed for

botanical examinations on the peninsula of Samana has been improved by a very fair local collection of plants numbering about two hundred species."

On January 27th, while Parry and Wright were in the field, the Commission resolved that Prof. Ward, the zoologist, make a trip along the coast in the direction of Cape Cabrón, "not exceeding ten days," and then go by land to Santo Domingo City "making a tour not exceeding a week," and that "Professor Wright and Mr. Brummel be requested to accompany Professor Ward, in order to complete the examination of the vegetable products of the peninsula." According to the official report, this party departed before Parry and the Blake party returned. Again, Wright's letters to Gray are in conflict with the published report, for Wright wrote that he sailed with the "Tennessee" and collected in the vicinity of Santo Domingo City while Brummel was traveling overland with Ward.

The Ward expedition left the Samaná anchorage and spent January 29th and 30th at Punta Cacao. They were prevented by high seas from rounding the tip of the Samaná peninsula and landed instead at "Port Francais" (Jan. 31) and went inland to Las Galeras and the Bahía del Rincón, returning to "Port Francais" the following day, February 1st. If this part of the report is true, it must have been a difficult and rapid trip and not a collecting expedition. On February 2nd, Ward and party, with Brummel along, crossed Samaná Bay, stopping at Cocal San Lorenzo. There are two specimens in the Wright, Parry and Brummel series attributed to San Lorenzo and these must have been gathered by Brummel. The party was in Savana de la Mar on February 3rd and then proceeded up the Yuna river on February 4th and 5th to Almacen (February 6th). They traveled overland to San Francisco de Macoris and on to La Vega and Cotui, all on February 7th, and on to Cevicos (February 8th), through the mountains of eastern Hispaniola to Savana la Grande, and arrived at Santo Domingo City on February 9th.

Meanwhile aboard the "Tennessee," anchored in very rough waters off Santo Domingo City, on February 4th the Commission asked Blake to make geological investigations about the capital and to organize an expedition to cross the central range of mountains to Puerto Plata, in a period not to exceed two weeks. Wright was to accompany him and to report on the vegetation of the interior. In the same resolution Parry was directed to examine the area around Santo Domingo City and to report. Wright's letters reveal that Parry was still suffering from a cold and that Wright took extended walks around Santo Domingo City; his letters describe the vegetation in considerable detail. On February 8th the report reveals that Blake accepted the directive to cross the island but that the time allotted was extended and the rendezvous time in Puerto Plata was set for March 1st.

On February 9th the botanists attached to the Commission were literally going in all directions. Parry and members of the Commission were on a leisurely trip by boat fifteen miles up the Río Ozama and then another 15 miles up a branch to the westward before returning in the late afternoon. Wright's letters and notes indicate that his party headed westward to the

Río Haina to begin a trek across the island. Brummel and party returned to Santo Domingo City on that day and apparently remained aboard the "Tennessee" to write up their report entitled, "Notes on the agricultural resources of Samana Peninsula and the Vega Real." There is a suggestion that Brummel did not collect botanical specimens on his trip with the Ward party, and his report is in contrast to others published. It is written in the most general terms and contains only one botanical scientific name. Brummel's name does not appear again in the official report of the activities of the Commission.

While the Blake party, including Wright, left Santo Domingo City to make their way to Puerto Plata, the Commission, with Parry and Brummel, remained in Santo Domingo City and concluded its work. The cutter "Nantasket" left the capital anchorage on February 14th for Puerto Plata, where some members of the Commission were to proceed inland to La Vega, meet the Blake-Wright party in Puerto Plata on March 1st and then rendezvous with the "Tennessee" at Port au Prince on March 7th. Other members of the Commission, with Parry and apparently Brummel on board, sailed with the "Tennessee" on February 14th, arriving at Ocoa Bay on the 23rd. Members of the Commission went inland to the town of Azua, and the "Wright, Parry and Brummel" specimens from Azua must have been collected by Parry or possibly Parry and Brummel during that visit. The "Tennessee" left Ocoa Bay on February 28th and arrived at Port au Prince on March 9th.

WRIGHT'S TRIP FROM SANTO DOMINGO CITY
TO PUERTO PLATA

Wright's manuscript of the "Flora Domingensis" carries many references to plants collected at "interior savannas," "wet vallies of the interior," "pine woods of the interior," most with dates of collections and a few plants with specific geographical locations. The official report, however, gives barometric readings with dates and places. It is possible to coördinate these two sets of data to derive the following itinerary of the crossing of Hispaniola.

February 9, Santo Domingo City, Río Haina, Santa Rosa, Arroyo Lebrun.
February 10–11, Madrigal.
February 12, Arroyo Los Guananitos, La Puerta.
February 13, Loma Laguneta, El Aguacate.
February 14, Río Maimon, Hato del Banao.
February 15, Arroyo Yuma, Río Yuna, Río Jima.
February 16, La Vega.
February 17, La Vega.
February 18, Santo Cerro.
February 18–19, Moca.
February 21–25, Santiago (February 23. Río Yaqui del Norte).
February 26–28, Arrenquillo River, El Limón, Loma de Bajabonico.
March 1–3, Puerto Plata.

Even with modern roads, this trip of about 105 airline miles would be an arduous one by foot or by horseback. In 1871, with few established paths, these deep with the mud remaining from the rainy season, it was an heroic undertaking in the time allotted for the 60-year-old Wright. A reporter who had come by boat to Puerto Plata to visit La Vega commented, "The only road from Puerto Plata to the interior is a bridle path to Santiago. In a direct line Santiago is only 18 miles, but by path it is 60 miles." He comments that the rainy season was scarcely over and that the paths were muddy and slippery. On his arrival in Puerto Plata, Wright received instructions to report on his trip immediately. His pique clearly shows in the first paragraph of his report. "The journey was made at a season of the year when fewest plants are in flower and not many in fruit. Called to join this Commission almost at a moment's warning, no time was afforded to obtain books suitable or sufficient to determine the plants found there; and the only books brought were left on the ship from a desire to reduce the luggage to the smallest possible dimensions. Moreover, no time could be saved to examine the plants in their fresh state, and to study them carefully, without neglecting the specimens gathered, by the careful preservation of which they might be more critically examined at a future time. Even the inquiries for the vernacular names of trees met with received unsatisfactory answers. The muleteers and guide seemed to know few of the trees of the mountain regions. Even when inquiries were addressed to the inhabitants, answers, whether thoughtless or intentional, so absurdly wrong were given that I despaired of gaining much reliable information which would serve to connect with certainty the vernacular names of the plants with their scientific ones. A more particular report must consequently be postponed till a critical examination of the specimens can be made." This proved to be a forecast of trouble to come.

The rendezvous at Port au Prince between the "Nantasket" and the "Tennessee" occurred on March 9th. This date is also recorded as the departure date for Kingston, Jamaica, where the "Tennessee" arrived March 11th. The "Nantasket" apparently returned to Puerto Rico or to Saint Thomas. While the "Tennessee" re-coaled in Kingston harbor, Wright had the opportunity of visiting the government Forestry Station at Cinchona in the Blue Mountains. He refers in later letters to his knowledge of the growth of quinine trees in Jamaica. It was in this area that Wright must have collected an unnumbered specimen of *Vaccinium meridionale* (us) which has bothered monographers. The species is not known from Hispaniola but does occur in the vicinity of Cinchona.

From Jamaica the "Tennessee" proceeded to Charleston, South Carolina, arriving there March 26th. The Commission held meetings aboard the ship en route and on March 19th, while at sea between Cape San Antonio de Cuba and Key West, they resolved "that the collections made by the scientific gentlemen who have accompanied this expedition be inventoried by them and deposited in the Smithsonian Institution, subject to the disposition of Congress." That all was not harmonious in the acceptance of this resolution is attested by the comment in the official

report, "During the discussion of said resolution the Commission took a recess until 7 o'clock p.m." Whether Parry wanted the specimens for the herbarium in his charge at the Department of Agriculture or whether Wright felt his collections, or all of them, should come to the Gray Herbarium for his study can not be resolved. In any case, the issue was not settled amicably, as is obvious from a note in the official report regarding a meeting of the Commission at the Arlington Hotel, Washington, D.C., on April 3, 1871. It is noted there that the Commission "received the following letter dated April 3 from Joseph Henry, Secretary of the Smithsonian Institution: 'Sir: On reply to the inquiry you make as to the disposition of specimens collected at the expense or under the auspices of the United States Government, I have the honor to inform you that, by the law of Congress organizing the Smithsonian Institution, it is the official curator of all collections of natural history, geology, etc. belonging to the United States, and that in accordance with this enactment all the specimens collected by the Wilkes, Gilliss, Rodgers, Perry and other naval expeditions, and the Pacific Railroad Boundary and geological surveys, are now in its custody.

" 'I may further state that an annual allowance is made by Congress for the preservation and exhibition of these and such other collections as may be made, and also for the distribution of the duplicates to academies, colleges and public museums.

" 'I am, very respectfully, your obedient servant,' . . ."

Thus, at the end of the Commission's report, the fate of the collections, as well as the responsibility for working them up, remains unclear.

The "Tennessee" arrived at Charleston, South Carolina, on March 26th and put ashore the heads of the Commission and several of the scientists, including Parry, who went to Washington. Wright remained on board as the "Tennessee" sailed to the port of New York. John Torrey wrote about this trip to Asa Gray on April 1, 1871. "Wright made his appearance at the office about noon today. He came directly from the Tennessee — which has been ever since the Santo Domingo Commissioners were landed at Charleston in reaching New York. She had expended all her coal and was unable to get up from the Quarantine to the city. He was quite disgusted with the ship and the miserable quarters — or rather filthy den that they had put him in — it being the very worst in the whole vessel. H . . . took him out to dine and although he would take nothing but plain beefsteak said it was the best dinner that he had eaten since he left for S. Dom. This afternoon that good man (I do like him) left for Wethersfield. It will probably be some days before he goes to Cambridge — for his wardrobe needs replenishing and he wishes to attend to some matters at home." Torrey also added, "I have not heard from Parry since his return. It seems that he has all of Wright's S. Dom. plants as well as his own — and it is understood that you will have the bulk of the collections, although they are not very bulky." Later letters proved incorrect the implication in the last sentence that Parry then had in his possession the specimens collected.

CHARLES WRIGHT AND ASA GRAY

It is not clear when Wright returned to Cambridge, how the collections finally reached the Gray Herbarium, or, in fact, how it was determined that Wright was to identify the collections which were then to become the property of the Department of Agriculture.

On June 5, 1871, Gray wrote to Wright at Wethersfield, "Will you do up the San Domingo plants for 8 dollars a page? . . . If you come and set to work with me I shall be pleased & you shall take time to distribute your San Domingo plants. If you study them for Parry or Washington — that will take ½ your time for some months. But 8 dollars a page for 80 pages or so would fairly pay. What presses me most is work in the Garden seeing to things & names and I much wish you would take hold and help an over worked fellow."

It was during these months that Gray was deeply concerned over the condition of the Botanical Garden in Cambridge. Without adequate funds to employ the number, or even the quality, of people required by the garden, Gray was seeking the devoted individual who would work for the small sum of money available.

On June 8th, Gray wrote two letters to Wright. In the first he stated, "Nothing therefore was meant on my part but to tell you the coast is so nearly clear here that you could do something if you wished either for Herbarium or for San Domingo coll. on your own hook." In the evening Gray wrote again, "Dear Wright. Let me go on. My *bete noire* here is the garden," and he elaborated on the problems of financing the herbarium work and the care of the garden. He continued in the letter to Wright, "You prefer to be Herbarium Curator, and I wish I could keep an herb. curator pure and simple, and it is just in your way. But the Herbarium fund yields only 850 dollars which is nearly all needed to run the establishment. And I must pay for most of the aid I could get out of my pocket. I could do something that way, and I would, if only I had the Garden off my mind."

Apparently Wright misunderstood Gray's interest in giving the Garden primary consideration as some reflection on his own taxonomic ability, for Gray was forced to explain in a letter to Wright dated June 28th, "As to the way you are doing up Cuban Botany, I do not find fault with it. I think, with you, that you are doing about the best possible thing under the circumstances. The only thing that you may justly complain of me for, I think, is my sensitiveness and *pooh-poohing* new species making in families where the old species are yet all in a jumble and where I have thought that you could not yet tell what were new and what old. I dare say I have been too impatient about it, and I see I have hurt your feelings somewhat, which I am sorry for. I only meant: take time & pains to clear up the old ones in the books, and get a better assurance, if you can, about the proposed new ones. But, after all, it is wrong and foolish in me to worry myself, or you, about them.

"You will have more experience of the sort in the working up of your

San Domingo coll. But if we can get time to refer doubtful cases to say Oliver at Kew, and some one at Paris (where they have many old San Domingo plants), I suppose you may get them pretty straight.

"I suppose these collections will keep you pretty busy this summer. But I hope you can complete the incorporation of the Ind. Or. residue . . ."

Wright apparently was reassured, and he appears to have been working on the collections in the early fall of 1871.

THE FATE OF THE COLLECTIONS

Wright did not have the collections in his possession when he left the "Tennessee" in New York on April 1. On April 11, Parry wrote to Gray, "You will see Wright soon and get particulars. I do not think he was treated as his services deserved but perhaps Prof. White was not to blame. It was a badly arranged affair but Wright has at least the satisfaction of knowing that he did his duty faithfully and the results will show that he deserved better treatment. Our so called *assistant*? (Wright knows who I mean) neglected his duty to the last. I left him in charge of the heavy boxes on the ship to dry and he took the 1st. boat for land and they are still on the ship. Have written to the Agr. Dept. agent to hurry them off. This delays me sorting out the collection as I intended to do at once. Tell Wright to write me as soon as he arrives at Cambridge."

This letter suggests that all was not well on the expedition and that the relations between the "botanists" were not completely harmonious. Apparently Wright was mistreated and Brummel was not exactly an asset. The letter also suggests that Parry intended to sort out the collections. Since all the specimens I have seen bear labels stating, "Distributed by the U.S. Department of Agriculture," it is clear that the specimens did not go to the Smithsonian Institution at that time and that Parry must have had the labels prepared.

Although correspondence between Parry and Wright and Parry and Gray is referred to in many of Gray's letters, such letters are not available for reference. Gray did write to Charles Wright on June 8th of Parry's intended visit to Cambridge soon after the 20th and also reported that "your 2 S. Domingo boxes are in my back kitchen." Torrey's earlier comment suggests that the two boxes represent both Parry's and Wright's collections and that they were in Cambridge for study by Wright and Gray.

Wright apparently worked over the collection during the summer and early fall of 1871. One specimen from Azua was selected as an unnamed new genus and species of the Polygalaceae. Regrettably no specimens of this taxon were cited by number under the detailed description given in the "Flora Domingensis." I have been unable to find any specimens to which this description might refer in any American herbarium. In a letter dated September 15, 1871, Oliver, of Kew, wrote to Asa Gray, "I have delayed a few weeks in replying to your note with San Domingo fragment wishing to show it to Mr. Bentham before reporting. Unfortunately I have

little to tell. The free or possibly free stamens and anther cells make it awkward for the Polygalaceae which seems after all the best place for it. *Loxopterygium* and allied genera of the Sapindaceae won't do. I keep the scrap but will return it at a word from you." There is no way of knowing if the "scrap" was the entire specimen of the new genus or if any material was retained by Gray where it is filed. Gray acknowledged Oliver's letter on October 16, 1871. "Receive a hasty line to thank you in Wright's name for your report on the little San Domingo puzzle . . . tho you leave it a puzzle still. Keep the scrap. I send by the Darwin Junior, a small parcel for Herbarium chiefly San Domingo plants. There are 40 to 60 of these which are puzzles or dubious or 'n. sp.' of Wright — in whose determinations I have small confidence. But unless I can tell him what a thing is, I can rarely stop him from printing. Could you, as you lay out for the *Herb*. just report on them as far as you can, without too much trouble. I have never looked at one of them — no time.

"The collection as a whole is meagre & poor. But there are some things worth your having. I am going to take his collection and will send in any duplicates which you are likely to care for. The greater part are common tropical rubbish."

Oliver received this shipment in November, examined it and reported on a part of the collection in December. Gray, in turn, acknowledged Oliver's assistance in a letter of January 7, 1872.

The ferns and their allies from the collection were sent by Wright to D. C. Eaton, in New Haven, Connecticut. Eaton gave these plants his own set of numbers (1–38) and reported the identifications in a memorandum dated October 22, 1871. Wright's manuscript flora has incorporated both the Oliver and the Eaton determinations. The manuscript therefore must have been prepared in early 1872, for Wright returned to his Wethersfield farm for the spring plowing. On September 16, 1872, Wright wrote to Gray that he knew Sereno Watson was to be his successor, and, although he needed the employment and would sorely miss the income, he hoped Watson would be able to do the work well.

Wright died in 1885. Asa Gray reported in a necrology of Wright that after the Santo Domingo expedition, "a large part of several years was passed at Cambridge, taking part of the work of the Gray Herbarium; and one winter was passed at the Bussey Institution." I can find no records stating specifically why the manuscript was put aside and never finished. Wright's presence in Cambridge suggests there was an opportunity for him to complete it, but perhaps an explanation for his failure to do so can be found in other episodes which followed the completion of the Commission of Inquiry.

WRIGHT'S EXPERIENCES ON THE EXPEDITION

Torrey's letter to Asa Gray, previously quoted, suggested that Wright was mistreated on the expedition but that he did his job faithfully. Charles Wright wrote to Asa Gray on January 31, 1871, and February 5, 1871,

from Santo Domingo. In these letters are bits of information which explain Torrey's comments, as well as some of the episodes which occurred after the expedition was over.

It seems clear that Wright made the trip with the idea in mind of extending the observations he had made in earlier trips to Cuba. It is also possible that Wright planned to stay in Santo Domingo after the departure of the Commission or to return at a later date. In one letter Wright stated, "If I were to conclude to make any considerable stay, I should expect that somebody, you or foreign botanists or our government or all would back me up strongly with moral and pecuniary support, otherwise it would be unwise for me to embark in such a labor. After a few days' examination of the vicinity of Santo Domingo City I shall be better able to decide what to do." He was encouraged by several local people to stay and continue botanical work, and he received offers of hospitality and support from residents of Santo Domingo. However, Wright's enthusiasm was dampened by the accommodations of the "Tennessee" and the attitude of the Commission. Wright, at 60 years of age, was the "oldest of all the attachés of the Commission," he wrote Gray. Nevertheless, he was regarded as a junior staff member and assigned some of the poorest quarters and mess facilities on the boat. He reported, "I have not been satisfied with my location in a mess. We are distributed among the different messes — On the back deck is the ward room mess, the middies' mess and the various forward officers' messes. With one of these I was placed while all the boys, loafers, etc., nearly are in the ward room or above . . . It was a mere accident no doubt, perhaps it was wisely ordered so, as I am better able to rough it than said boys, loafers etc." After Wright's return, Torrey referred to Wright's accommodations as the "miserable quarters — or rather filthy den that they had put him in — it being the very worst in the whole vessel," and Parry wrote that he did not think Wright "was treated as his services deserved."

From Wright's letters one also learns more of Brummel. On the first trip at Samaná, Wright reported, "At Samana the land arises abruptly into very broken hills — no mangrove swamps, no level plains, one marshy flat which might have given more of its peculiar plants had we all been waders like me. Parry didn't do much and his assistant, less, unless it be windwise and in this he can beat old Eobus. Parry came on board with a bad cold and cough which he has only now shaken off. His assistant is a gardener and is more intent (and not too much so) on gathering seeds and roots than on making specimens." Torrey, too, in later correspondence with Gray, referred to "that incompetent gardener who went with the Santo Domingo expedition."

While Wright and Parry were gathering specimens as vouchers for their observations, their activities to this end were not valued. Wright wrote Gray, "Then Wade couldn't see the use of gathering so many weeds, etc., etc. It seems to me that the Commissioners care very little for any branch of science that don't have some regard to the precious metals, coral or logwood (Mr. White has already a mahogany tree of his own on board)."

When these comments are added to those previously cited and the events which involved Parry shortly after his return, it is no wonder that the botanical results of the Commission of Inquiry were not approached with enthusiasm by the participants or their associates.

PARRY'S EXPERIENCES IMMEDIATELY
AFTER THE EXPEDITION

Parry returned to his position as botanist for the U.S. Department of Agriculture in early July, 1871. On September 19th, Parry wrote to Gray of attitudes and dicta by his superior that were making his professional life difficult and his personal correspondence with Gray a violation of department rules. On September 27th he was summarily dismissed from his position. Both Torrey and Gray were incensed and decided to take action on Parry's behalf. On October 3, 1871, Gray wrote to Torrey, apparently in response to a letter from him, "Parry wrote to me about the outrageous conduct. The first thing to do is for his friends to require to know the reasons why. To write an article for the papers would only express our feeling, and do no good, perhaps harm. When you go to Washington, see Prof. Henry — you two go to the commissioner yourselves directly, and ask him what it all means — asking it in reference to scientific interests of the country as well as in justice to Dr. Parry. If there is no show of reason, — as I suppose, and the commissioner will not rectify the injustice — then go to higher authorities. If your Academy is of any good it might look into it. If things are to go on let us have the facts, and we will bring them before the scientific public, and, if deserved denounce the Agricultural bureau — as being — what Capron alone seemed to be raising it from — an institution for wasting vast sums of money." A long correspondence continued between Torrey and Gray and other American and foreign botanists concerning Parry's unwarranted discharge, and a plan of action evolved. The pertinent correspondence between Gray as spokesman for the outstanding botanists and the Commissioner of Agriculture regarding Parry's dismissal was eventually published in the *American Naturalist* (January, 1872), and the letters, as well as the opinions, were the subject of articles and editorials in other American (e.g., Am. Jour. Sci. III. 3: 315–318. 1872) and foreign scientific journals. Parry was not reinstated, however, and returned to his collecting expeditions in the West. Torrey and Gray corresponded about the possible successor to Parry, and, in a letter of November 4, 1871, Torrey expressed concern for the official attitude toward the herbarium specimens Parry had accumulated and the herbarium itself. "A new man coming in — especially if it were that incompetent gardener who went with the Santo Domingo expedition (and who Parry thinks had had much to do with his removal) might do a great deal of harm." Regarding the Santo Domingo collections Torrey wrote on January 16, 1872, "Wright ought not to let the Agric. Dept. have a set until a botanist, whom Prof. Henry and those who he may consult approve of his appointment."

The office of government botanist remained vacant until April, 1872, when George Vasey, a botanist well known to Torrey and Gray, was appointed. The fate of Parry and the feud with the Commissioner of Agriculture continued, however, for on receipt of a letter from Vasey, Gray wrote to Torrey on April 27, 1872, "I answered Vasey's letter in substance thus: 'It would give me pleasure to correspond with you personally, as I always have done though I have not time now to do so to any great extent. But as Botanist of Agriculture Depart. I meet a difficulty. I understand that you are not yourself allowed to correspond with me directly. All letters as Botanist must be signed by the Commissioner etc. Now I imagine it would not be altogether pleasant nor satisfactory for me to correspond with the commissioner etc.' — Hoisting the commissioner with his own petard? I was in some hopes that Vasey might reply that he had permission to correspond with me directly, which would have been nice." There is no further correspondence between Vasey and Gray in the historical files of the Gray Herbarium. Watts remained Commissioner of Agriculture for about ten years, and Vasey occupied the post of botanist until he died in office in 1893. Vasey apparently had learned his lesson from Parry's experience, for in his first annual report (Report of the Commissioner of Agriculture for the year 1872. Government Printing Office, 1874) Vasey states, "Deeming it an important part of the work of this division to give attention to inquiries for information on questions relating to botany, and particularly to practical and economic botany, the investigation of such questions has occupied a considerable amount of time of the present officer of the division."

In the annual reports available to me, including the historical report following Vasey's death (1894), there is no mention of the specimens of the Commission of Inquiry to Santo Domingo.

Brummel, too, had dropped from sight, with no further mention of him in the available reports of the U.S. Department of Agriculture.

DATA ON THE COLLECTIONS

There is no information available from the records of the Gray Herbarium, the Smithsonian Institution, or the U.S. Department of Agriculture to indicate when the collections of the Santo Domingo Commission of Inquiry were returned from Cambridge, nor is it clear who distributed the duplicates. These points, however, may be made with certainty:

1. The most complete set of specimens is currently in the U.S. National Herbarium.

2. The set in the Gray Herbarium, though small in number, appears to represent unicates or duplicates of specimens Wright considered to be new species or unusual records. Generally speaking, these specimens are smaller in size, truly scraps, in comparison.

3. The specimens in the Kew Herbarium were sent by Asa Gray to Oliver before the full collection was distributed. These, too, represent the new species, unusual records or questionable determinations.

4. Very few specimens have been found in the herbarium of the New York Botanical Garden.

5. A few specimens have been cited by monographers from the herbarium of the Missouri Botanical Garden. These have been checked in the families Loranthaceae, Amaryllidaceae and Vitaceae. It is possible that a larger number are there representing other families. The correspondence of Engelmann is preserved at the Missouri Botanical Garden and this has been checked. There are several letters to and from Parry indicating that Parry was notified of his position on the Commission of Inquiry several months prior to the departure of the expedition. Engelmann asked particularly that Parry collect specimens of the Cactaceae for morphological study. Engelmann was not satisfied with the results, however, for, on June 8, 1871, he wrote to Parry, "Got your different things at last. One by one. But there is confusion with me or with you. Your send. 'Cereus No. 1 smooth top.' 'wood ring' also marked No. 1. But the flowers are marked No. 2, 3. Flowers, Azua and Port au Prince all in same envelope and mixed, so which is Azua and which Port au Prince. I can not make out. Now whether No. 1 and No. 2 are the same. And Jamaica and all San Domingo seem to be beautifully mixed up. There is a living plant of a Cereus, 8 ribbed, 'flowers and notes to come.' These disjointed bits are all puzzles and rob me of a good deal of time uselessly make confusion. I am too dull to unriddle them. I shall return your notes in a few days."

A comparable complaint could have been made regarding the collections of *Agave*. In one packet mounted with an *Agave* specimen there is a note from Parry, "Capsule of Agave (I think from San Domingo) I remember it was difficult to find *mature capsules*. Do Agave like Yuccas require insect agency? In Florida the Agaves flower very freely but never perfect fruit C.C.P." The words "I think" were later crossed out. Another packet of *Agave* carries, in Parry's handwriting, the annotation "capsules and seeds from different places, San Domingo. Parry."

6. A single specimen of *Cestrum* was cited by Francey from the herbarium of the Chicago Natural History Museum.

7. The number of specimens cited by Urban and other German botanists in the various volumes of the *Symbolae Antillanae* and in *Pflanzenreich* suggest that some specimens were, or are, in the Berlin Herbarium. The collections cited are rarely those numbers sent to Oliver at Kew. Only one collection which was annotated by Urban has been seen in an American herbarium.

8. The specimens of ferns and their allies were sent to D. C. Eaton by Wright and bear Eaton's numbers. Dr. John Reeder kindly had the Eaton herbarium checked for me, and, as Series II indicates, the majority of the numbers listed in Eaton's correspondence with Wright are represented in the Yale University Herbarium. A smaller number of the fern specimens are in the National Herbarium; none has been found in the Gray Herbarium.

9. Wright must have seen the entire collection in one place at one

time. His manuscript "Flora Domingensis" contains the only reference to places, dates and numbers applicable to the entire collection.

10. No field book has been found relating to this collection. Annotations by both Wright and Gray in the manuscript refer to missing "tickets," suggesting that no field book was made.

11. The packets on some, but not all, of the herbarium sheets contain slips of paper with information on the date and location of the collections. These may be the "tickets." These slips are all in the handwriting of Charles Wright and are comparable in size and details to those commonly found with Wright's Cuban collections.

12. The numbers on the specimens and in the manuscript indicate that the collection was sorted to family and to genus before the numbering was done. Wright's manuscript indicates a number for the collection and then the location. In some cases a single number refers to a specimen in flower from one location and to another in fruit made at a different location miles away and some days later. As many as seven different collections, localities and dates are recorded to one number. This was the system employed by Asa Gray and apparently followed by Charles Wright.

13. Not all of the collections or the numbers referred to in the manuscript have been located.

14. All of the collections bear the same label of a blue-gray color stating that the specimens were distributed by the U.S. Department of Agriculture.

15. Nearly all of the sheets on which the collections are mounted are characteristically discolored, suggesting that the specimens were all poisoned at one time with bichloride of mercury. This is true of Wright, Parry, and Brummel specimens as seen in four different herbaria.

The specimens of the collection made by Wright, Parry, and Brummel as seen in American herbaria were distributed without specific dates or locations. All bear names, including unpublished epithets, as given in Wright's manuscript. A very few of the sheets have been annotated. In general, the specimens have been of questionable value for lack of appropriate data. Not even the size of the collection has been known accurately. Eaton numbered 38 collections, specimens of which are in the Yale University and the U.S. National herbaria. Not all of the species given on the list sent by Eaton to Wright have been located.

The Wright manuscript contains numbers for 634 entries. However, 26 numbers are repeated or treated as "A," "B," or "X" entries. Thirteen numbers in the numerical sequence are not used in the manuscript. Several specific entries appear for which specimens are not cited. Occasionally, locations and/or dates are given for these entries, all of which refer to cultivated plants and so may represent observations. About a dozen specimens were found in the U.S. National Herbarium with data about the specimen in the packet, while Wright's manuscript stated "without ticket" and did not cite location or date. Thirteen specimens have been located, by chance, which are not cited in the manuscript and which carry no data. The specimen of *Vaccinium meridionale* previously mentioned is such a one, as is a sterile one of *"Juniperus gracilis"* (US). These

may be all or in part from Jamaica. The total collection by Wright, Parry, and Brummel must consist of about 688 numbers.

THE LOCATIONS AND DATE OF COLLECTION

The following alphabetical listing of localities may be useful in determining the geographic location, date, and probable collector of numbered specimens. It has been compiled from the official report of the expedition, from the Wright manuscript and from locality or date slips accompanying some of the specimens seen.

1. Aguacate, *Wright*, February 13, 1871.
2. Azua, *Parry*, February 23–28, 1871.
3. Bajabonico, *Wright*, February 26–28, 1871.
4. "Deep vallies of the interior." Between Santo Domingo City and Puerto Plata, *Wright*.
5. "Interior forests." Between Santo Domingo City and Puerto Plata, *Wright*.
6. "Interior savannahs." Between Santo Domingo City and Puerto Plata, probably between El Aguacate and the Río Jima, *Wright*, February 13–15, 1871.
7. La Vega, *Wright*, February 18, 1871.
8. La Vega to Moca, *Wright*, February 18, 1871.
9. Madrigal, many from Río Jaina at Madrigal, *Wright*, February 10, 1871.
10. Moca, *Wright*, February 18–19, 1871.
11. Moca to Santiago, *Wright*, February 20, 1871.
12. Ozama River, *Wright* and/or *Parry*, February 1–8, 1871.
13. Port au Prince, collector uncertain, probably *Parry*, March 9, 1871.
14. Port Francais, *Brummel*, January 31 or February 1, 1871.
15. Puerto Plata, *Wright*, March 1–3, 1871.
16. Río Guananito, *Wright*, February 12, 1871.
17. Río Jaina, *Wright*, February 10, 1871.
18. Río Vuelta, *Wright*, February 13, 1871.
19. Samaná, *Wright & Parry*, January 24–29, 1871.
20. Santo Domingo City, *Wright* and/or *Parry*, February 1–8, 1871.
21. Santo Domingo City to Puerto Plata, *Wright*, February 9–27, 1871.
22. San Lorenzo, *Brummel*, February 1, 1871.
23. San Soreijo [San Lorenzo?], Collector unknown, locality not found.
24. Santiago, *Wright*, February 21–25, 1871.
25. Santiago to Puerto Plata, *Wright*, February 24–27, 1871.
26. Savana de la Mar, *Brummel*, February 3, 1871.

IDENTIFICATION AND PRESENT LOCATION OF THE SPECIMENS

The following lists represent enumerations of the Wright, Parry and Brummel collections made while on the Commission of Inquiry to Santo Domingo. The specimens are cited in four series. The first numerical series (I) is that compiled from the Charles Wright manuscript "Flora Domingensis" now in the archives of the Gray Herbarium. The second numerical series (II) is that reported to Charles Wright by D. C. Eaton

(letter, in the Gray Herbarium, dated October 22, 1871) and consists of ferns, lycopods and selaginellas. The numbers given were assigned by Eaton. The third series (III) is unnumbered and represents specimens which were not included in the Wright manuscript and some of which were not collected in Santo Domingo. The fourth list (IV) is alphabetical and consists of species listed by Wright, primarily as observations. These are not numbered and as far as can be determined to the present are not represented by specimens.

In each list the names preceded by an asterisk (*) were considered by Wright to represent new species. Some of these had complete descriptions in the original manuscript. There are forty-one numbers so designated which represented twenty-seven new species. If the manuscript had been published in 1872 when prepared, thirteen of the species would be recognized today, for the specimens can be assigned to acceptable species described after that date. Eight of the species are in difficult groups or consist of inadequate material and so can not be accurately assigned at the present time. Wright, Parry, and Brummel collections are the holotypes of eleven species described by other authors since 1871.

Names which are given in quotation marks in the following lists have been taken directly from the Wright manuscript and validating specimens have not been seen. Only the generic name is given if the complete epithet has not been published elsewhere. The number following the specific name refers to the alphabetical list of locations and dates given above. If such a number is not given, the Wright manuscript either listed two or more specimens, localities and dates for one collection number or the data were missing from the manuscript. The location of specimens is designated in parentheses by standard herbarium abbreviations (Lanjouw & Stafleu). The specimens as designated have either been seen by the author or are reported to occur in that herbarium and are listed in the citation of specimens by monographers and others.

Not all of the specimens listed below are satisfactorily identified. Many of the genera concerned need revision. In the difficult genera of the Loranthaceae and in the genera *Eugenia* and *Psychotria* the Wright, Parry, and Brummel specimens I have seen are of poor quality and are inadequate for determination at the present time.

Numerical Series I

1. *"Nasturtium brevipes,"* 7
2. *Drymaria cordata,* 15 (US)
2B. *Sauvagesia erecta,* 6 (K, US)
3. *"Capparis cynophallophora,"* 25
4. *Capparis cynophallophora* (US)
4B. *Capparis baducca* (US)
5. *Hybanthus linearifolius* (US)
6. *"Anona* sp."
6B. *Oxandra lanceolata* (US)
7. *"Bocagea laurifolia"*
8. *Polygala longicaulis,* 6 (US)
8X. *Agave intermixta,*[1] 24 (GH, MO, US)
9. *Polygala paniculata,* 15 (US)
9X. *Agave antillarum,* 24 (US)
10. *Polygala penaea,* 24 (US)
11. *Securidaca virgata,* 20 (US)
12. *Samyda dodecandra,* 20 (US)
13. *Xylosma coriaceum,* 15 (US)
14. *Xylosma coriaceum,* 15 (US)
15. *Casearia comocladia,* (US)
16. *Casearia hirsuta,* 11 (US)
17. *Casearia arborea,* 4 (US)
18. *Conocarpus erecta,* 15 (US)
19. *Conocarpus erecta* var. *sericea,* 13 (US)
20. *Combretum laxum* (US)
20X. *Ochroma pyramidale* (US)

21. *Trichilia pallida* (K, US)
22. *Xylosma coriaceum,* 15 (US)
23. *Rhacoma crossopetalum,* 15 (US)
23B. *Schafferia frutescens,* 15 (US)
24. *Rhacoma ilicifolia,* 6 (US)
25. *Begonia brachypoda,* 25 (US)
26. *Melothria guadalupensis* (K, US)
27. *Passiflora suberosa* (US)
28. *"Passiflora pallida"*
29. *Passiflora murucuja,* 19 (F, MO, US)
30. *Passiflora suberosa* (US)
31. *Anguira pedata* (US)
32. *Cayaponia racemosa* (US)
33. *Sechium edule* (US)
34. *Mormordica charantia* (US)
35. *Fevillea cordifolia* (US)
36. *"Turnera ulmifolia"*
36. *"Phaseolus clitorioides,"* 19
37. *"Piriqueta cistoides,"* 6
38. *"Malachra texana,"* 15
39. *Sida acuminata* (K, US)
40. *Sida hederaefolia* (US)
41. *Dalechampia scandens,* 2 (US)
41. *Rhacoma gonoclada,*[2] 20 (K)
42. *Wissadula amplissima,* 20 (US)

[1] Trelease studied the Wright, Parry, and Brummel material of *Agave*, noting that it was a mixed collection (Mem. Natl. Acad. Sci. 11: 31, 32, *pls. 41–43, 64.* 1913). Part of the collection was referred to *Agave antillarum* Descourt. and part was selected as the type of *Agave intermixta* Trelease. (Trelease had prepared a complete description of this species and a discussion of its affinities. Such a manuscript is currently in the herbarium of the Missouri Botanical Garden. For some unknown reason a much abbreviated description was given as a footnote in the reference cited above and the discussion was never published.) The single specimen in the Gray Herbarium is without number, but in a packet is a field note carrying most of the data given in the Wright manuscript. The same slip indicates that a specimen was sent to Dr. Engelmann and it is this specimen at the Missouri Botanical Garden which was designated as the holotype by Trelease. The collection was made on the bank of a stream near Santiago de los Caballeros on February 22, according to the field notes. In the manuscript Wright stated the collection was made on "steep hills" near Santiago.

The text for *Plate 43* in Trelease's monograph of the genus *Agave* in the West Indies suggests that the leaf margin included in *Figure 1* may be that of *Agave intermixta*. This illustration agrees with the leaf specimen in the Gray Herbarium which is mounted on the same sheet with the flowers typical of *Agave intermixta* and not *Agave antillarum*.

[2] Wright used the name *"Myginda gonioclada,* n. sp.," in his manuscript. Kuntze cited this name in synonymy when transferring the species to the genus *Crossopetalum* (Rev. Gen. 1: 116. 1891). Kuntze does not indicate where he saw the name Wright

43. *Malvastrum spicatum*, 20 (US)
44. "*Malachra capitata*," 19
45. *Centrosema virginiana*, 19 (US)
45. "*Melochia tomentosa*"
46. *Sida ciliaris* (US)
47. *Sida rhombifolia*, 21 (US)
48. *Pithecellobium circinale*, 2 (GH, US)
49. *Bauhinia divaricata*, 13 (US)
50. *Acacia tortuosa* (US)
51. *Rhacoma gonoclada*, 2 (K, US)
52. *Caesalpinia pauciflora*, 13 (US)
53. *Corynella dubia*, 13 (GH, US)
54. *Rhodopis planisiliqua* (GH, US)
54. *Guarea trichiloides*, 21 (US)
55. blank
56. blank
57. *Vilmorinia glyciphylla*, 21 (GH, US)
58. *Calliandra portoricensis*, 20 (US)
59. "*Desmodium incanum*," 19
60. *Calopogonium caeruleum*, 20 (US)
60. "*Mimosa ceratonia*"
61. *Acacia lutea*, 20 (GH, US)
62. *Centrosema pubescens* (US)
63. "*Galactia cubensis*," 19
64. "*Aeschynomene sensitiva*," 19
65. "*Vigna luteola*," 19
66. "*Mimosa ceratonia*"
67. *Phaseolus adenanthera*, 19 (US)
68. *Inga vera*, 19 (K)
69. *Acacia lutea* (US)
70. *Crotalaria retusa*, 19 (US)
71. *Mucuna sloanei* (US)
72. "*Rhynchosia reticulata*"
73. *Cassia biflora*, 20 (GH, US)
74. *Albizia lebbeck* (US)
75. *Inga laurina*, 15 (US)
76. *Poitea galegoides*, 21 (US)
77. *Stylosanthes hamata*, 20 (US)
78. *Sophora tomentosa* (US)
79. "*Cassia diphylla*"
80. *Vilmorinia glyciphylla*, 21 (K)
81. *Desmanthus virgatus* (US)
81B. "*Anguria pedata*"

82. *Crotalaria verrucosa*, 15 (GH, US)
83. *Senegalia angustifolia*, 25 (US)
84. *Teramnus uncinatus* (US)
85. *Desmanthus virgatus* (US)
86. *Inga laurina* (US)
87. *Vilmorinia glyciphylla*, 21 (US)
88. *Corynella paucifolia*, 9 (K, US)
89. *Barbieria pinnata*, 21 (US)
90. "*Mimosa ceratonia*," 21
91. *Poitea galegoides*, 21 (US)
92. *Alysicarpus nummularifolius* (US)
93. *Poitea galegoides*, 21 (US)
94. *Desmodium adscendens*, 9 (US)
95. *Erythrina poeppigiana*, 9 (US)
96. *Pictetia spinifolia* var. *ternata*, 24 (US)
97. *Corynella paucifolia*, 24 (K, GH)
98. *Ateleia gummifera*, 24 (US)
99. *Poiretea scandens*, 21 (GH, US)
100. *Haematoxylon campechianum*, 20 (GH, US)
101. blank
102. *Hibiscus brasiliensis* (US)
103. *Pavonia spinifex*, 20 (US)
104. *Sida acuta* (US)
105. *Melochia nodiflora*, 19 (US)
105. *Sida rhombifolia*, 19 (US)
106. *Corchorus hirsutus* (US)
106A. "*Urena sinuata*"
107. *Helicteres jamaicensis* (US)
108. *Melochia tomentosa*, 13 (US)
109. "*Corchorus hirtus*," 21
110. *Waltheria americana*, 20 (US)
111. *Triumfetta lappulacea*, 19 (K, US)
111A. "*Triumfetta semitriloba*"
112. *Malpighia domingensis*, 24 (US)
113. *Stigmaphyllum lingulatum*, 24 (US)
114. *Stigmaphyllum ovatum*, 19 (US)
114A. "*Cordia laevigata*"
115. *Stigmaphyllum ovatum*, 19 (US)

coined. Oliver, in correspondence, reported Wright's new species to be similar to another specimen collected by Schomburgk at Azua. Urban finally described *Rhacoma gonoclada* (Symb. Ant. **5**: 75. 1904). He cited both the names used by Wright and Kuntze and indicated that he saw the specimen in the Kew Herbarium. The number "41" here duplicated from Wright's manuscript is probably an error for "51."

116. *Bourreria succulenta* (us)

117. *Byrsonima coriacea*, 1 (us)

118. *Bunchosia media*, 7 (us)

119. *Stigmaphyllum lingulatum*, 20 (us)

120. *Stigmaphyllum lingulatum*, 15 (us)

121. *Malpighia domingensis* [3] (us)

122. *Stigmaphyllum angulosum*, 20 (us)

123. *Triopteris ovata*, 13 (gh, us)

124. *Malpighia aquifolia*, 2 (us)

125. *Malpighia domingensis*, 20 (us)

126. *Thryallis glauca*, 20 (us)

127. "*Triopteris rigida*," 15

128. *Banara domingensis* (k, us)

129. "*Guarea trichilioides*," 19

130. *Picramnia pentandra* (us)

131. *Corchorus siliquosus* (us)

132. *Melochia pyramidata* (us)

133. *Colubrina ferruginosa*, 20 (us)

134. *Muntingia calabura* (us)

135. *Hydrocotyle hirsuta*, 20 (us)

136. *Dalbergia ecastophyllum*, 19 (us)

137. *Rondeletia berteriana*, 20 (gh, us)

138. "*Picramnia pentandra*"

139. *"*Myrtus (Eugenia*) sp. nov.," [4] 20

140. *Miconia racemosa*, 21 (us)

141. "*Miconia laevigata*," 19

142. *Clidemia hirta*, 19 (us)

143. *Miconia prasina*, 19 (us)

144. *Ossaea acuminata*, 2 (us)

145. "*Miconia nicotianafolia*," 2

146. *Acidanthera quadrata*, 6 (us)

147. *Miconia racemosa*, 21 (us)

148. *Nepsera aquatica*, 6 (us)

149. *Miconia laevigata*, 19 (us)

149A. "*Nepsera aquatica*," 6

150. *Miconia prasina*, 26 (us)

151. "*Miconia impetiolaris*," 19

151A. "*Casearia ilicifolia*"

152. *Picramnia pentandra* (us)

153. **Serjania polyphylla* (us)

154. *Paullinia pinnata*, 19 (us)

155. *Gouania lupuloides*, 19 (us)

156. *Gouania polygama*, 19 (us)

157. *Serjania polyphylla*, 19 (us)

158. *Rajania cordata* (us)

159. **Serjania sinuata*,[5] 25

160. *Securidaca virgata*, 19 (us)

161. *Allophylus rigidus*, 13 (us)

162. *Rourea surinamensis*, 21 (us)

163. *Eugenia pseudopsidium* var. *portoricensis*,[6] 20 (us)

164. *Mouriria domingensis*, 10 (us)

165. *Syzygium jambos* (us)

166. *Eugenia* aff. *umbellulifera*, 20 (us)

167. *Eugenia monticola* (us)

168. *Eugenia myrtoides*, 15 (us)

169. **Eugenia* sp. nov. (k)

170. **Eugenia* sp. nov.[7] (gh, us)

[3] Small selected this specimen as the holotype of *Malpighia domingensis* (N. Am. Fl. **25**: 156. 1910). According to the Wright manuscript, the specimen was collected on February 14, 1871, when Wright was in the area between Río Maimon and Hato del Banao. Collections *112* and *125* listed by Wright as the same were made at Santiago and Santo Domingo City respectively.

[4] Wright described this collection, citing also No. 166, as a new species. He reported "collected from bushes 10–15′ growing nearly on the site of the old city of SD hence it is as likely to be something introduced from abroad as to be indigenous. Feb. 30. The species seems most likely to belong to Berg's genus Myrcianthus or possibly to Myrtus." The date given is in error but no correction can be offered. Wright was in Puerto Plata on February 30th and he did not arrive in Santo Domingo City until January 31st in the earlier part of his trip.

[5] This collection was named "*Serjania apiculata* n. sp." by Wright. On the field label Wright reported the collecting locality to be between Santiago and Puerto Plata and the date, February 25. Radlkofer (Pflanzenr. IV. **165**(Heft 98a): 117. 1933) gave Wright's unpublished name and reported he saw a specimen in the Kew herbarium.

[6] This specimen bears the annotation, "determined by Urban."

[7] The collections *169* and *170* are cited in the Wright manuscript as new species with an unpublished name. Collection *169* was sent to Oliver at Kew. Both collections were made on February 18th and on that date Wright was between Santo-

171. *Ternstroemia peduncularis,* 21 (US)
172. *Ardisia escallonioides,*[8] (GH, K, US)
173. *"Prunus sphaerocarpa,"* 25
174. *Simaruba glauca,* 9 (US)
175. *Sesuvium portulacastrum* (US)
176. *Hydrocotyle umbellata,* 19 (US)
177. *Bourreria virgata* (US)
178. *Hirtella triandra,* 19 (US)
179. *Guaiacum officinale,* 2 (US)
180. *Lawsonia inermis* (US)
181. *Jussiaea leptocarpa,* 19 (K, US)
182. *Jussiaea leptocarpa,* 19 (US)
182A. *"Jussiaea salicifolia"*
183. *Jussiaea erecta,* 19 (US)
184. *Cissus caustica,* 8 (US)
185. *Ampelocissus robinsonii* (GH, K, MO, US)
186. *"Vitis sicyoides,"* 19
187. *Bursera simaruba,* 19 (US)
188. *Anacardium occidentale* (US)
189. **Comocladia dentata* (GH, K, US)
190. **Comocladia domingensis*[9] (US)
191. *Comocladia dodonaea,* 20 (US)
192. **Comocladia cuneata*[10] (K, US)
193. *Calophyllum brasiliensis* var. *antillanum,* 19 (US)
194. *Chrysobalanus icaco,* 23 (US)
195. *Eugenia pseudopsidium* var. *portoricensis,* 20 (US)
196. *Comocladia dodonaea,* 20 (GH, US)
197. *Tetragastris balsaminifera,* 9 (K, US)
198. *"Lagenaria vulgaris,"* 24

199. *Annona reticulata* (US)
200. *Mormordica charantia* (US)
201. *Chrysophyllum olivaeforme,* 20 (US)
201. *Centrosema virginiana* (US)
202. *Chrysophyllum argenteum,* 9 (US)
203. **Chrysophyllum olivaeforme* (K, GH)
204. **Psychotria pinularis,* 15 (US)
205. *Psychotria tenuifolia* (US)
206. *Psychotria domingensis,* 19 (US)
207. *Psychotria grandis,* 19 (US)
208. *"Psychotria uliginosa,"* 19
209. *Psychotria berteriana* (GH, US)
210. *Palicourea barbinervia* (US)
211. *Psychotria brachiata,* 21 (US)
212. *Hamelia patens,* 19 (US)
213. *Palicourea domingensis* (US)
214. *Chiococca alba* (US)
215. *"Ernodea litoralis,"* 15
216. *"Ixorea ferrea,"* 15
217. *Psychotria revoluta,* 15 (US)
218. *Micromeria viminea,* 13 (US)
219. *"Rauwolfia nitida,"* 20
220. *Ernodea litoralis,* 15 (US)
221. *Diodia maritima,* 15 (US)
222. *Cornutia pyramidata,* 15 (US)
223. *Borreria ocimoides* (US)
224. *Bourreria domingensis,* 20 (US)
225. *Guettarda scabra* (US)
226. *Chione exserta,* 9 (GH)
227. *Psychotria revoluta,* 9 (US)
228. *Borreria verticillata,* 17 (US)
229. *"Borreria parviflora,"* 9
230. *Manettia calycosa,* 21 (US)
231. *Borreria ocimoides* (US)

Cerro and Moca. The two specimens of *170* which I have seen can not be identified with certainty at this time.

[8] This collection was identified and cited by Mez (Pflanzenr. IV. **236**(Heft 9): 81. 1902) who apparently saw the specimen at Kew. Urban (Symb. Ant. **8**: 520. 1921) and Moscoso (Cat. Flor. Dom. 471, 1943) repeated the reference. Wright's manuscript noted that "no ticket" was available to give location and date of the collection.

[9] The Wright manuscript notes that this collection has a "mixed ticket." The locality given is Santo Domingo City but the data apply to a species of *Piper.* Britton selected this collection as the type of his new species (Bull. Torrey Club **37**: 350. 1910).

[10] Britton selected the specimen at the U.S. National Herbarium as the type of his new species *Comocladia acuminata* (Bull. Torrey Club **37**: 349. 1910). Since this epithet is a later homonym, he renamed it *Comocladia cuneata* (Bull. Torrey Club **41**: 9. 1914). Wright's manuscript reported the collection was without data.

232. *Borreria laevis*, 9 (us)
233. *Erithallis vaccinaefolia*, 9 (us)
234. *Randia aculeata* (gh, k)
235. *Antirrhoea lucida*, 25 (us)
236. *Parathesis serrulata*, 19 (us)
237. **Guettarda preneloupii* [11] (k, us)
238. *Guettarda scabra*, 21 (us)
239. *Sauvagesia erecta*, 21 (us)
239. *Tournefortia scabra*, 21 (us)
240. *Tournefortia scabra*, 21 (us)
240. *Diodia sarmentosa* (us)
241. **Randia erythrocarpa*, 13 (us)
242. *Catesbaea parvifolia*, 2 (us)
243. *"Ixorea ferrea,"* 15
244. *Psychotria brachiata*, 21 (us)
245. *Erithallis fruticosa* (k)
246. *Randia parvifolia* (us)
247. *Eupatorium* sp.,[12] 13 (us)
248. **Gochnatia oligantha* (Urban) Howard, comb. nov.[13] (gh, k)
249. *Enhydra sessilis*, 19 (us)
250. blank
251. *Eleutheranthera ruderalis*, 7 (us)
252. *Eupatorium odoratum*, 20 (us)
253. *Mikania scandens*, 19 (us)
254. *Mikania cordifolia*, 19 (us)

254. *Luffa cylindrica* (us)
255. *Salmea scandens*, 19 (us)
256. *"Wedelia carnosa,"* 19
257. *Pacourina edulis*, 19 (gh, us)
258. *Borrichia arborescens* (us)
259. *Melanthera Buchii* 19 (us)
260. *Erigeron jamaicensis* (us)
261. **Chaptalia primulacea,*[14] 15 (gh, k)
262. *Pluchea odorata* (us)
263. *Porophyllum ellipticum* (us)
264. *Ageratum conyzoides* (us)
265. *Eupatorium obtusissimum* (us)
266. *Verbesina alata* (us)
267. *Tithonia rotundifolia* (us)
268. **Senecio haitiensis*, 25 (k, us)
269. *Chaptalia nutans*, 6 (us)
270. *Vernonia racemosa*, 11 (us)
271. *Senecio plumbeus*, 15 (us)
272. *Erigeron jamaicensis*, 10 (us)
273. *Vernonia sprengeliana*, 20 (us)
274. *Vernonia sprengeliana*, 20 (us)
275. *Eupatorium obtusissimum*, 15 (us)
276. *Synedrella nodiflora*, 19 (us)
277. *Salmea scandens*, 19 (us)
278. *Wedelia gracilis*, 21 (us)
279. *Vernonia buxifolia*, 21 (us)

[11] Wright's manuscript gives two dates, February 3 and 9, for this collection made between Santo Domingo City and Puerto Plata. On both dates Wright was in the vicinity of Santo Domingo City.

[12] Wright used an unpublished specific name (referring to the incised margin of the leaves) which he attributed to Grisebach. I have been unable to identify accurately the material cited.

[13] Urban described this as *Anastraphia oligantha* (Symb. Ant. **3**: 417. 1903), the basionym of the new combination above, citing in synonymy *Anastraphia paucifloscula* used by Wright in his manuscript and on the specimens of this number. Wright's invalid name was also used by Hitchcock (Ann. Rep. Mo. Bot. Gard. **4**: 102. 1893). Urban cited only a collection by Wright, Parry, and Brummel, without giving it a number. In a later publication (*loc. cit.* **8**: 746. 1921) Urban refers to "Wright, Parry and Brummel 248." This collection must be considered the type, and, although Urban does not indicate the source of his material, he must have examined the specimen at Kew which is to be considered the holotype. Roy Jervis has annotated the specimen in the Gray Herbarium with a name transferring the species to the genus *Gochnatia*. This combination was not published. Wright indicated in his manuscript that the field label with location and date are missing.

[14] Wright annotated this collection with an unpublished name referring to the long leaves. He sent a specimen to Oliver who suggested it had affinities with *Chaptalia longiflora*. Greene described the collection as *Chaptalia primulacea* (Leafl. Bot. Obs. **1**: 195. 1906) selecting a specimen in the U.S. National Herbarium as the holotype. Robinson annotated both the Gray Herbarium specimen and the Greene publication suggesting that the species is the same as *Chaptalia membranacea* Urban. The collection was made on March 2, at Puerto Plata.

280. *Pectis carthusianorum*, 6 (US)
281. *"Chrysanthellum procumbens,"* 10
282. *Pectis procumbens*, 6 (US)
282. *Hieracium gronovii* (GH)
283. blank
284. **Isodorea pungens*,[15] 20 (GH, K, US)
285. *Wallenia laurifolia*, 19 (US)
286. *Wallenia laurifolia*, 19 (US)
287. *Erithallis fruticosa*, 19 (US)
288. *Randia aculeata* (US)
289. *Gonzalagunia spicata*, 19 (US)
290. *Chiococca alba*, 19 (US)
291. *Psychotria revoluta* (US)
292. *"Palicourea guianensis"*
292. *Palicourea crocea*, 19 (US)
293. *Palicourea barbinerve* (US)
294. *Palicourea riparia*, 19 (US)
294B. *Palicourea crocea* (US)
295. *"Psychotria berteriana,"* 19
296. *Psychotria pubescens*, 19 (US)
297. **"Psychotria* sp. nov.,"[16] 9 (GH)
297. *Psychotria microdon*, 15 (US)
298. *Diodia rigida*, 6 (US)
299. *Spermacoce tenuior*, 15 (US)
300. *"Spermacoce* sp.,"[17] 19
301. **Lobelia salicina*, 19 (K, US)
302. *Lobelia cliffortiana*, 20 (US)
303. *"Conradia reticulata,"* 4
304. *"Ardisia crenulata,"* 19
305. *Dipholis salicifolia*, 19 (US)
306. *"Jacquinia ruscifolia,"* 24
307. *Citharexylum fruticosum* (US)
308. *Jacquinia Eggersii* (US)
308. *Citharexylum fruticosum* (US)

309. *Hippocratea volubilis* (US)
310. *Cestrum macrophyllum*, 19 (US)
311. *Solanum polyacanthum*, 21 (US)
312. *"Solanum callicarpaefolium"*
313. *Cestrum diurnum*[18] (F)
314. *"Cordia globosa"*
315. *Bourreria virgata*, 24 (US)
316. *Cordia curassavica* (US)
317. *"Nama jamaicensis"*
318. *Buchnera elongata*, 6 (US)
319. *Cordia lima*, 7 (US)
320. *"Melochia serrata"*
321. *Cordia serrata*, 13 (US)
322. *Cordia sebestena* (K, US)
323. *Wigandia urens*, 16 (US)
324. *Cordia nitida* (US)
325. *"Pavonia typhalea"*
326. *Scoparia dulcis*, 20 (US)
327. blank
328. *"Bourreria virgata,"* 24
329. *Cordia globosa* (US)
330. *Lantana involucrata*, 15 (US)
331. *"Capraria biflora"*
332. *Bacopa stricta*, (GH, US)
333. *Gerardia fasciculata*, 6 (US)
334. *Lobelia domingensis*, 6 (K, US)
335. *Ammania latifolia*, 21 (US)
336. *Cordia sulcata*, 19 (GH, US)
337. *Lantana camara* var. *mista*,[19] 19
338. *"Heliotropium parviflorum,"* 20
339. blank
340. *"Scutellaria havanensis,"* 19
341. *Ocimum gratissimum* (US)
342. *Leonotis nepetaefolia*, 19 (US)
343. *Hyptis pectinata*, 19 (US)
344. *Scutellaria havanensis*, 15 (US)

[15] In his manuscript Wright recognized this collection as a "new species" which he called *Isodorea pungens* citing in synonymy *Ernodea pungens* Lam. Robinson had access to the Wright manuscript and the specimen in the Gray Herbarium, although he neither cited the specimen nor gave Wright credit in making the new combination *Isodorea pungens* (Lam.) Robinson (Proc. Amer. Acad. Arts Sci. **45**: 401. 1910). Wright's specimen was collected on cliffs by the river, near Santo Domingo City, on February 3.

[16] This material is inadequate for accurate determination but appears to be *Psychotria pinularis*.

[17] The Wright manuscript ascribes a specific name attributed to Jacquin to this collection. I can find no reference to the publication of this epithet.

[18] Wright's manuscript cites *"Solanum verbascifolium"* for this number; however, Francey in his monograph of *Cestrum* (Candollea **6**: 286. 1936) cites a specimen from the Chicago Natural History Museum as given above.

[19] This collection, as well as *357*, was cited by Moldenke (An alphabetized list of citations **3**: 1146. 1949) as identified. The herbarium source of the material is not stated.

345. blank
346. *Hyptis suaveolens,* 19 (US)
347. *Hyptis capitata,* 19 (US)
348. *Hyptis lantanifolia,* 9 (US)
349. *Ocimum gratissimum,* 19 (US)
350. "*Salvia occidentalis*"
351. *Hyptis americana,* 19 (US)
352. *Hyptis pectinata,* 19 (US)
353. *Stachytarpheta jamaicensis,* 19 (GH, US)
354. *Priva lappulacea,* 20 (US)
355. *Petitia domingensis,* 7 (US)
356. *Clerodendron aculeatum* (US)
357. "*Cornutia pyramidata,*" 15
358. *Acalypha alopecuroides* (US)
359. *Acalypha setosa,* 20 (GH, US)
360. *Blechum brownei* (US)
361. *Dicliptera assurgens,* 20 (US)
362. *Ruellia tuberosa* (US)
363. *Teliostachya alopecuroides,* 9 (US)
364. *Barleriola solanifolia,* 2 (US)
365. *Ruellia coccinea,* 19 (K, US)
366. *Justicia pectoralis* (US)
367. *Justicia sessilis,* 20 (US)
368. *Ruellia domingensis,* 21 (US)
369. *Justicia pectoralis,* 19 (GH, US)
370. *Cordia serrata,* 21 (US)
371. *Jacquemontia pentantha,* 20 (US)
372. *Jacquemontia nodiflora* (US)
373. *Merremia umbellata,* 20 (US)
374. "*Ipomoea umbellata,*" 20
375. *Rivea corymbosa,* 20 (US)
376. *Merremia quinquefolia* (US)
377. *Jacquemontia nodiflora* (US)
378. *Ipomoea eriosperma* (US)
379. blank
380. "*Ipomoea campanulata,*" 19
381. "*Ipomoea cathartica*"
382. "*Ipomoea fastigiata*"
383. "*Ipomoea cathartica*"
384. *Ipomoea acuminata* (US)
385. *Ipomoea acuminata* (US)
386. "*Ipomoea fastigata*"

387. *Ipomoea setifera,*[20] 19 (GH, K)
388. *Ipomoea tiliacea* (US)
389. *Ipomoea tiliacea* (US)
390. *Rivea campanulata,* 19 (US)
391. *Cuscuta americana,* 20 (US)
392. "*Limnanthemum humboldtianum,*" 10
393. *Schultesia heterophylla,* 6 (US)
394. *Micranthemum nuttallii,* 18 (US)
394B. *"*Micranthemum* sp. nov.,*"[21] (GH, K)
395. "*Utricularia pusilla*"
395. "*Tabernaemontana citrifolia,* 6 (US)
396. "*Tabernaemontana neriifolia*"
396. *Psychotria undata* (GH, US)
397. "*Ipomoea fastigiata*"
397. *Rhabdadenia berterii,* 21 (US)
398. "*Tabernaemontana neriifolia,*" 15
399. *Distictis lactiflora* (K)
400. *Calatropis procera* (US)
401. *Isotoma longiflora,* 19 (US)
402. *Rhabdadenia paludosa,* 19 (US)
403. *Asclepias nivea* (US)
404. "*Echites umbellata*"
405. *Echites umbellata* (US)
406. *Urechites lutea,* 15 (US)
407. *Rauvolfia nitida,* 20 (US)
408. *Anagadenia berterii,* 21 (US)
409. "*Echites repens,*" 19
410. *Exostema longiflorum* (US)
411. "*Metastelma leptocladon,*" 21
412. "*Piper dilatatum,*" 21
412. *Metastelma Picardae* (US)
413. *Tabernaemontana amygdalifolia,* 17 (US)
414. "*Cestrum pallidum,*" 20
415. *Nectandra antillana,* 9 (US)
416. "*Phoebe montana,*" 21
417. blank
418. *Linociera domingensis,* 21 (US)
419. "*Nectandra willdenoviana*"
420. *Ocotea leucoxylon,* 19 (US)
421. "*Nectandra willdenoviana*"

[20] This collection bears an unpublished specific name relating to the peninsula of Samaná where the specimen was collected January 27, 1871. Neither this specimen nor any of the other Convolvulaceae here have been cited by House or other monographers of the family.

[21] Wright had prepared a complete description for publication but was unable to supply data on the date or location of the collection. The genus requires a monographic treatment before the cited specimens can be determined.

422. *Licaria triandra*, 10 (US)

423. *Trichostigma   octandrum*,   21 (US)

424. *"Pisonia aculeata,"* 9

425. *Pisonia aculeata*, 25 (US)

426. *Rapanea guianensis* (US)

427. *Rapanea ferruginea*, 9 (GH, US)

428. *"Chamissoa altissima,"* 20

429. *Iresine angustifolia*, 20 (US)

430. *Alternanthera geniculata* (US)

431. *"Rousselia lappulacea,"* 19

432. *Pilea repens*, 19 (US)

433. *Fleurya aestuans* (US)

434. *Urera baccifera*, 19 (US)

435. *Ficus trigonata*, 8 (US)

436. *Ficus citrifolia*, 8 (US)

437. *Ficus citrifolia*, 8 (US)

438. *Ficus trigonata*, 10 (US)

439. *"Marcgravia umbellata"*

440. *Piper aduncum*, 19 (US)

441. *Piper aduncum*, 19 (US)

442. *Piper dilatatum* (US)

443. *Piper jacquemontanum*,[22] 19 (GH, US)

444. *Piper marginatum*, 21 (MO, US)

445. *Piper hispaniolae* [23] (US)

446. *Piper parryanum*,[24] 19 (US)

447. *Piper dilatatum* (US)

448. *Piper parryanum*, 19 (GH, MO, US)

449. *Peperomia distachya*, 19 (US)

450. *"Peperomia caulibarbis"*

451. *Peperomia serpens*, 19 (US)

452. *Peperomia serpens*,[25] 19

453. *Peperomia glabella*, 19 (US)

454. *Dendrophthora   marmeladensis*, 21 (US)

455. *Dendrophthora   marmeladensis*, 21 (US)

456. *"Dendróphthora wrightii,"* 21

457. *Dendrophthora flagelliformis*, 15 (US)

458. *Phoradendron anceps*, 15 (US)

459. **Phoradendron cerinocarpum*

459A. *Phoradendron chrysocarpum* [26] (US)

460. *Phoradendron   hexastichum*, 21 (US)

461. **Phoradendron mucronatum* (GH, K, US)

462. *Phoradendron   mucronatum*, 9 (US)

463. *Dendrophthora flagelliformis*, 15 (US)

464. *Phoradendron   dichotomum*, 10 (US)

465. *Phoradendron   piperoides*,[27] 25 (US)

466. *Phoradendron   dichotomum*, 24 (US)

467. *Phoradendron   antillarum*, 21 (US)

468. *Dendropemon purpureus* (US)

468A. *Dendropemon uniflorus* (US)

469. **Dendropemon   alatus* (GH, K, US)

470. **Dendropemon   alatus*, 2 (GH, K, US)

[22] This collection was cited by Trelease (Repert. Sp. Nov. **23**: 307. 1927) as given above.

[23] Trelease selected the specimen in the U.S. National Herbarium as the holotype of this species which he described as new (*loc. cit.* 309). Wright's manuscript gives one collection number but two locations for the material: Puerto Plata, February 26, and Samaná, January 27. I have been unable to determine the original locality of the holotype.

[24] Trelease cited *Wright, Parry & Brummel 446* and *448* in describing this species as new (*loc. cit.* 311). Number *446* was selected as the holotype in the U.S. National Herbarium. Both collections were made in Samaná on January 28, 1871.

[25] Trelease (*loc. cit.* 323) cited this collection number without indicating the location of the specimen.

[26] *Wright, Parry & Brummel 459* is cited by Trelease (The Genus *Phoradendron*. Univ. Ill. Bull. **13**: 139. 1916) as the holotype of *Phoradendron cerinocarpum*. The specific epithet is attributed to Wright and occurs in the manuscript. Unfortunately, the numerical designation in the Loranthaceae is badly mixed. Number *459* is reported to have been collected between Moca and Santiago, on February 21, and on the road from Santo Domingo City to Puerto Plata, on February 13, a date when Wright was in the vicinity of Loma Laguneta and El Aguacate.

[27] Cited under this name by Trelease (*loc. cit.* 147).

471. *Suriana maritima*, 13 (US)
472. *Coccoloba swartzii*, 21 (GH, K, US)
473. *Coccoloba swartzii*, 21 (GH, US)
474. **Coccoloba fuertesii*, 21 (GH, K, US)
475. *Coccoloba nodosa, 21 (GH, K, NY, US)
476. **Coccoloba incrassata*, 2 (GH, K, US)
477. **Coccoloba diversifolia* (GH, US)
478. *Exostema caribaeum*, 2 (US)
479. *Pisonia aculeata* (US)
480. *Cyathula achryanthoides*, 19 (US)
481. *Fleurya aestuans*, 21 (US)
482. *Pilea repens*, 17 (US)
483. *Rousselia humilis*, 19 (US)
484. *Tabebuia berteri*, 6 (US)
485. *Tabebuia berteri* (US)
486. *Forsteronia corymbosa* (US)
487. *Rhabdadenia paludosa* (US)
488. "*Echites repens*," 19
489. *"*Guettarda* sp. nov." [28]
490. *Jatropha gossypifolia* (US)
491. *Adelia ricinella*, 2 (US)
492. *Acalypha setosa*, 19 (GH)
493. *Acalypha glechomifolia* (US)
494. *Clerodendron aculeatum* (US)
495. *Argithamnia candicans*, 15 (US)
496. "*Phyllanthus nobilis*," 25
497. "*Drypetes alba*," 19
497. *Psychotria revoluta*, 19 (K, US)
498. *Drypetes alba* (US)
499. "*Drypetes* sp. nov.," [29] 15
500. *Drypetes alba*, 15 (US)
501. *Drypetes alba*, 21 (US)

502. *Ilex aff. *macfadyenii*,[30] 21 (US)
503. *Croton origanifolius* (GH, US)
504. "*Croton flavens*," 2
505. *Croton pallidus* (GH)
506. *Croton discolor*, 24 (US)
507. *Croton linearis*, 13 (US)
508. *Euphorbia prostrata* (US)
509. *Euphorbia buxifolia*, 13 (US)
510. "*Euphorbia heterophylla*," 15
511. *Euphorbia hirta*, 19 (US)
512. *Euphorbia heterophylla*, 15 (US)
513. *Solanum antillarum*, 21 (US)
514. *Peperomia obtusifolia*,[31] 9 (US)
515. *Erithallis fruticosa*, 15 (K, US)
516. *Stigmaphyllon lingulatum* (US)
517. *Exothea paniculata*, 19 (US)
518. *Cuphea micrantha[32] (K)
519. *Cuphea parsonsia*, 16 (US)
520. "*Miconia fothergilla*," 9
521. *Miconia macrophylla*, 1 (US)
522. *Tetrazygia bicolor*, 6 (US)
523. *Heterotrichum umbellatum*, 21 (US)
524. *Ossaea acuminata*, 6 (US)
525. *Miconia elata*, 21 (US)
526. *Miconia rubiginosa*, 9 (GH, US)
527. *Dieffenbachia seguine*, 19 (US)
528. *Costus cylindricus*, 19 (GH, US)
529. *Pistia stratiotes*, 7 (US)
530. *Hypoxis erecta*, 6 (US)
531. *Heteranthera limosa*, 6 (US)
531A. *Heteranthera spicata* (US)
532. *Cipura palludosa*, 6 (US)
533. *Anthurium scandens*, 4 (US)
534. *Tillandsia valenzuelana* (US)
535. "*Anthurium* sp.," [33] 19
536. "*Anthurium* sp.," [33] 19
537. *Cissampelos pareira* (US)

[28] No material has been seen of this number. Wright described a new species in his manuscript citing *237* and *489*. The former has been referred to *Guettarda preneloupii*. The collections were made near Santo Domingo City on February 3rd and 9th.

[29] Wright compared his material with "*Drypetes incurva* Mull." and suggested it was perhaps a distinct species. The specimen was collected at Puerto Plata on February 26. No material has been located.

[30] Wright's notes indicate that he collected this specimen on February 15 when he travelled in the vicinity of the Arroyo Yuma, the Río Yuna and the Río Jima.

[31] Trelease had annotated this sheet with a new specific name honoring Brummel and indicated this as the type. The name apparently was never published.

[32] This specimen has not been cited by monographers of the Lythraceae. The unpublished specific name referred to Santo Domingo. The specimen was collected "in the savannas of the interior at Madrigal" on February 11, 1871.

[33] Wright uses in his manuscript a name attributed to Schott which appears to be unpublished. No description is given and no specimens have been located.

538. *Dioscorea polygonoides*, 19 (US)
539. *Smilax populnea*, 15 (US)
540. *Smilax domingensis* (US)
541. *Callisia monandra*, 20 (US)
542. *Tradescantia geniculata* (US)
543. *Commelina elegans*, 19 (GH, US)
544. *Commelina elegans* (US)
545. *Commelina diffusa*, 20 (US)
546. *Callisia monandra*, 21 (US)
547. *Thrinax parviflora*, 20 (US)
548. blank
549. *Coccothrinax* sp.,[34] 14 (US)
550. *Copernicia* sp.,[34] 2 (US)
551. *Pleurothallis gelida*, 5 (US)
552. *Epidendrum rigidum*, 19 (US)
553. *"Aeranthus* sp.,'' 9
554. *Tetramicra parviflora* (GH, US)
555. blank
556. *Ponthieva glandulosa*, 5 (US)
557. *"Spiranthes elata,"* 21
557A. *Pelexia* sp. (US)
558. *"Pelexia setacea"*
559. *Malaxis spicata*, 19 (US)
560. *Syringodium filiforme*, 15 (US)
561. *"Epidendrum bifidum,"* 5
562. *Ponthieva glandulosa*, 6 (US)
563. *Epidendrum wrightii*, 21 (US)
564. *"Epidendrum broughtonioides,"* 6
565. *"Polystachya luteola"*
566. *Oncidium variegatum*, 19 (US)
566A. *"Epidendrum bifidum"*
567. *"Cranichis muscosa"*
568. *"Spiranthes apiculata,"* 6
569. *Ponthieva ekmanii*, 5 (US)
570. *"Epidendrum nocturnum,"* 22
571. *Epidendrum strobuliferum*, 19 (US)
572. *"Aeranthus* sp.,'' 19
573. *Epidendrum difforme*, 19 (US)
574. *Bletia patula*, 5 (GH, US)
574A. *Bletia patula* (US)
575. *Xyris caroliniana*, 6 (US)
576. *Cyperus peruviana*, 9 (US)
577. *Cyperus densicaespitosus*, 19 (US)
578. *"Rhynchospora florida,"* 21
579. *Cyperus haspan*, 6 (US)
580. *"Scirpus exiguus,"* 6

581. *Rhynchospora barbata* (US)
582. *"*Eleocharis* sp. nov." [35]
583. *Rhynchospora barbata* (US)
584. *"Fimbristylis brizoides,"* 6
585. *"Rhynchospora barbata"*
586. blank
587. *Eleocharis capitata*, 9 (US)
588. *"Rhynchospora vahliana"*
589. *"Rhynchospora glauca,"* 19
590. *Fimbristylis dichotoma*, 6 (US)
591. *Rhynchospora barbata* (US)
592. *Eleocharis retroflexa*, 19 (US)
593. *Cyperus nanus*, 15 (US)
594. *Scleria secans*, 19 (US)
595. *Cyperus elegans*, 15 (US)
596. *Eleocharis geniculata* (US)
597. *"Eleocharis plantagineus,"* 19
598. *Fuirena umbellata*, 19 (US)
599. *Rhynchospora pusilla*, 19 (US)
600. *Eleocharis chaetaria*, 6 (US)
601. *"Dichromena pusilla,"* 19
602. *"Kyllingia brevifolia,"* 19
603. *Mayaca fluviatilis*, 6 (US)
604. *"Carex scabrella,"* 15
605. *Pharus latifolia* (US)
606. *"Pharus latifolius,"* 19
607. *Paspalum laxum*, 19 (US)
608. *Ichnanthus pallens*, 19 (US)
609. *"Paspalum compressum,"* 19
610. *Chloris sagraeana*, 19 (US)
611. *Eragrostis ciliaris*, 19 (US)
612. *Chloris inflata* (US)
613. *"Orthopogon labiaceus,"* 19
614. *Lasiacis patentiflora*, 19 (US)
615. *Lasiacis sloanei*, 19 (US)
616. *Hyparrhenia hirta*, 12 (US)
617. *Paspalum laxum* (US)
618. *Paspalum laxum* (US)
619. *Phragmites communis* (US)
620. *Paspalum virgatum*, 19 (US)
621. *Cenchrus brownii* (US)
622. *Digitaria villosa* (US)
623. *Reynaudia filiformis*, 6 (US)
624. *"Cenchrus viridis,"* 19
624A. *Panicum stenodes*, 6 (US)
625. *Andropogon virgatus*, 6 (US)
626. *Arundinella confinus*, 6 (US)
627. *Panicum diffusum*, 21 (US)
628. *"Tricholaena insularis"*

[34] The available material of these palms is inadequate for accurate determination.
[35] A specimen collected in "springy places in savannas of the interior, Feb. 10," according to Wright's manuscript. No specimens have been located.

629. *Andropogon bicornis* (US)
630. *Tricholaena insularis* (US)
630. *Paspalum paniculatum* (US)
631. *Andropogon saccharoides, 6 (US)
632. *Andropogon saccharoides, 6 (GH, US)
633. "*Panicum dichotomum*," 21
634. *Digitaria horizontalis*, 19 (US)

Series II

1. "*Lycopodium mexicanum*"
2. *Ananthacorus angustifolia* (US)
3. *Adiantum deltoideum* (US, YU)
4. *Adiantum cristatum* (US, YU)
5. *Adiantum obliquum* (US, YU)
6. *Lindsaea portoricensis* (US)
7. *Adiantum fragile* (US, YU)
8. *Dryopteris serra* (US, YU)
9. *Pteris longifolia* (US, YU)
10. *Pityrogramma tartarea* (US, YU)
11. "*Gleichenia pubescens*"
12. *Dryopteris tetragona* (YU)
13. *Polypodium salicifolium* (US)
14. *Polypodium astrolepis* (US)
15. *Aspidium scolopendrioides* (YU)
16. *Tectaria heracleifolia* (US)
17. *Tectaria martinicensis* (US, YU)
18. *Pityrogramma sulphurea* (US, YU)
19. *Trichomanes krausii* (US, YU)
20. *Trichomanes lineolatum* (US)
21. *Trichomanes krausii* (US)
22. *Anemia hirsuta* (YU)
23. *Anemia adiantifolia* (YU)
24. *Cheilanthes microphylla* (US, YU)
25. *Asplenium serratum* (US, YU)
26. *Alsophila aquilina* (US)
27. *Cyclopeltis semicordata* (US, YU)
28. *Asplenium dentatum* (US)
29. *Pityrogramma calomelaena* (US, YU)
30. *Asplenium cristatum* (US)
31. *Dryopteris dentata* (US)
32. *Cyathea arborea* (US, YU)
33. *Odontosoria aculeata* (US, YU)
34. *Alsophila aquilina* (US)
35. *Selaginella plumosa* (US, YU)
36. *Lycopodium cernuum* (US, YU)
37. "*Lycopodium complanatum*"

Series III

Aristolochia aff. *pentandra* [36] (K)
Bidens leucantha (US)
Guazuma ulmifolia (US)
Hura crepitans, 19 (US)
Hymenaea courbaril (US)
Ipomoea batatas, 19 (US)
Ipomoea pes-caprae (US)
Iresine celosia (US)
Juniperus gracilis (US)
Mimosa pudica (US)
Nopalea cochenillifera, 10 (GH)
Pinus occidentalis (US)
Vaccinium meridionale [37] (US)
Zamia pumila (US)

Series IV

Ananas sativus, 19
Annona cherimola
Annona muricata
Annona palustris
Sebastiana corniculata, 9

[36] Determination by Oliver, 1871.
[37] Probably collected near Cinchona, Jamaica.

COMPARATIVE ANATOMY OF THE LEAF-BEARING
CACTACEAE, II

STRUCTURE AND DISTRIBUTION OF SCLERENCHYMA IN THE
PHLOEM OF PERESKIA, PERESKIOPSIS AND QUIABENTIA

I. W. Bailey [1]

Various forms of sclerenchyma, as commonly defined (e.g., Eames
and MacDaniels,[2] Esau [3]), occur in the leaf-bearing genera *Pereskia*,
Pereskiopsis and *Quiabentia*: (1) libriform fibers are present in the sec-
ondary xylem of stems and roots, (2) strands of aggregated slender fibers
in the primary phloem of stems, (3) concentric layers of sclereids in
periderm of stems and roots, and (4) highly diversified forms of sclereids
.in the secondary phloem of *Pereskia*. It is significant in this connection
that, under normal circumstances, sclerenchyma does not occur in the
leaves and pith of the three genera. The libriform fibers of the xylem and
the sclereids of the periderm will be dealt with in subsequent papers of
this series. In the following pages, I shall confine myself to a discussion
of sclerenchymatous elements that are formed in the phloem of the three
genera.

The leaf-bearing Cactaceae have mixtures of very dense and exceed-
ingly soft tissues and are difficult to section. After experimenting with
various methods of embedding following preliminary softening with such
reagents as hydrofluoric acid, I have in general obtained the most useful
preparations by sectioning stems and roots of living plants or specimens
preserved in formalin-acetic-alcohol fixative without the use of preliminary
treatments. Although the transverse and longitudinal sections thus ob-
tained with an adequately sharpened knife and sliding microtome are
relatively thick, they are suitable for critical visual examination. Further-
more, they have the advantage, not only of being obtained simply and
rapidly, but also of retaining starch, crystals, and other cell inclusions
which may be much modified or eliminated during softening and em-
bedding. It must be admitted, however, that they are not of the best
quality for photographic illustration.

FIBERS OF THE PRIMARY PHLOEM

Strands of aggregated primary phloem fibers occur in the stems of
Pereskiopsis and *Quiabentia*, as well as in those of *Pereskia* (Figs. 1a,

[2] Eames, A. J., and L. H. MacDaniels. An introduction to plant anatomy. Ed. 2.
McGraw-Hill Book Co., N. Y., 1947.
[3] Esau, K. Plant Anatomy. John Wiley and Sons, N. Y., 1953.

7a). Particularly in the more succulent parts of *Quiabentia* and some species of *Pereskiopsis*, the number of fibers in each strand tends to be reduced. Furthermore, the maturation of fibers in the former genera tends to be precocious, whereas in *Pereskia* the final stages of maturation may at times be delayed until more or less extensive cambial activity has occurred.

The individual fibers are slender, elongated elements of the general external form illustrated in FIG. 12. Their diameter commonly varies from 20 to 50 microns and their length from a few hundred microns to more than 2000. The marked variability in length occurs, not only in strands from different parts of a plant, but also in adjacent fibers of a single strand. Fibers having normal, lignified secondary walls may be internally septate or nonseptate, but they do not store starch as the corresponding septate and nonseptate libriform fibers of the secondary xylem so commonly do. Those of *Quiabentia* and *Pereskiopsis* tend to form relatively thick secondary walls and contain few if any internal septa at maturity (FIG. 13). On the contrary, in the case of *Pereskia*, many of the fibers have thinner secondary walls and are internally septate (FIG. 14). It is significant that part or all of such septate fibers in a strand may ultimately form internally a chain of sclereids having lignified, multi-layered walls (FIG. 15). Occasionally, the protoplast of one of the sclereids may divide leading to the formation of two smaller sclereids included within a larger one. This unusual phenomenon of cells-within-cells, which is of infrequent and sporadic occurrence in septate libriform fibers of secondary xylem (FIG. 6) is of considerable interest from physiological and developmental points of view and merits detailed investigation. For example, the two or three successive waves of lignified wall formation indicate that lignification is not necessarily an immediate precursor of loss of potentialities or degeneration of the protoplast as has sometimes been assumed.

The orientation of cellulosic microfibrils in the broad central or S_2 layer of the secondary wall of septate and nonseptate fibers, of both the primary phloem and the secondary xylem, varies from approximate parallelism to the long axis of the cell to helices of varying pitch. Clues to such variations may be obtained by studying the orientation of the slit-like pits, by the distribution of slip-planes, and by examining thin transverse, longitudinal and diagonal sections in polarized light. In FIG. 6, a very thin, perfectly transverse section in polarized light between crossed nicols, the tenuous outer or S_1 layer of the four adjacent fibers is strongly birefringent. The broad central or S_2 is dark, whereas in longitudinal section it is birefringent. This indicates that the orientation of cellulosic microfibrils in the S_2 layer of the secondary wall is approximately longitudinal, as does the orientation of slit-like pits and the distribution of slip-planes visible in longitudinal sections. Internal to the normal S_1 and S_2 layers of the septate fibers in FIG. 6 are transverse sections of the multilayered walls of included sclereids, the cellulosic layers of which are alternatingly birefringent and dark in polarized light. In such transverse sections as

Fig. 6, it is not possible to determine whether the original secondary wall of the fibers has a tenuous S_3 layer or not. It should be emphasized in this connection that these cells-within-cells provide interesting material for analysis by electron microscopy.

Occasionally a cell of prosenchymatous form on the margins of a strand of primary phloem fibers divides precociously before secondary wall formation (Fig. 16). Subsequently such cells may form a chain of sclereids (Fig. 17) comparable developmentally to wood parenchyma strands or the strands of short tracheids that occur in certain of the Pinaceae. (See glossary of terms used in describing woods.[4])

FORMS OF SCLERENCHYMA IN THE
SECONDARY PHLOEM OF PERESKIA

Under normal conditions of growth, schlerenchyma does not occur in the cortex and secondary phloem of stems and roots of species of *Pereskiopsis* and *Quiabentia* that I have investigated. In striking contrast to absence in these genera is the occurrence (particularly in larger stems and roots) of more or less numerous and diversified forms of sclereids in the secondary phloem of all species of *Pereskia* (including *Rhodocactus*) of which I have examined adequate material. The form and the distribution of the sclereids is consistently different in three distinct categories of putative species of *Pereskia*.

1. Species with Diffusely Distributed Sclereids
in the Secondary Phloem

In *Pereskia aculeata* Mill., *P. pititache* Karw., *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, *P. nicoyana* Web., *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd., the sclereids in the secondary phloem of large stems and roots are abundant and diffusely distributed (Figs. 1–3). In transverse sections, these cells, which vary in diameter from less than 18 to more than 100 microns, have conspicuously multilayered secondary walls which frequently occlude the lumen of the cell. As indicated in Fig. 5, the numerous layers of the secondary wall (which may exceed 50 in the case of the largest cells) are alternatingly birefringent and dark or feebly birefringent in polarized light. (Compare with the internal sclereids shown in Fig. 6.)

As seen in longitudinal sections (Fig. 4), these cells have a much elongated prosenchymatous form, the most slender ones having a length of a few hundred microns, whereas the broadest ones may attain at times a length of more than two thousand microns. In many of these cells the lumen tends to be occluded toward the ends of the cells and to be much reduced in the central part (Fig. 18). However, some of the cells having thinner multilayered walls become septate and may subsequently form a

[4] International Association of Wood Anatomists. Glossary of terms used in describing woods. Tropical Woods 36: 1933.

chain of shorter sclereids internally. The pits of the secondary wall tend to be restricted to the broadest central part of the cell (FIG. 18) and to be more or less irregularly distributed. It is significant in this connection that many of the pits are of the so-called ramiform type characteristic of many sclereids (FIG. 19). From a developmental point of view, such pits are actually of a coalescing, rather than of a ramifying type, for, the orifices of two or more simple pits in the first-formed layers of the secondary wall unite to form a single opening in the inner or last-formed layers of the wall.

A limited number of sclereids may occur at times in the expanded cortex of much enlarged stems (FIG. 1b). These vary from cubical to various bizarre forms. However, where they have a conspicuously longer axis, it is oriented at various angles and not consistently parallel to the long axis of the stem.

2. Species with Sclereids Aggregated in Longitudinally Oriented Clusters

In large older stems of *Pereskia sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., *P. corrugata* Cutak, and *P. tampicana* Web. aggregations of sclereids commonly occur in the secondary phloem (FIGS. 7, 8). These aggregations, as seen in longitudinal sections of the stem, are of elongated form, frequently of more or less fusiform outline (FIG. 9), and are oriented parallel to the long axis of the stem. They are composed of sclereids which vary markedly in size, form and complexity of internal structure. Although in general the sclereids have a more or less extensively elongated form (with their major axis oriented parallel to the long axis of the stem), they frequently assume aberrant shapes (FIG. 23), apparently due to pressures exerted by adjacent cells during the earlier stages of their excessive enlargement. In some cases, the sclereids have a thick, lignified, multilayered wall and a much restricted or occluded lumen (FIG. 20). In other cases, the sclereids first form a multilayered wall followed by transverse septation and subsequent differentiation of two, three, or more smaller sclereids internally (FIG. 21). Particularly in the case of the largest sclereids, which may attain a diameter of 200 microns and a length of 1000 microns, the protoplasts of the included sclereids may in turn divide, leading to the formation of a second set of still smaller sclereids (FIG. 22). Such compound sclereids of the cells-within-cell type commonly assume many diverse forms internally depending upon the timing and frequency of internal divisions and upon the frequency of diagonally rather than transversely oriented septa. Therefore, in macerations of the phloem, it may be difficult at times to determine with certainty whether certain of the smaller isolated sclereids developed directly from less expanded parenchymatous elements of the secondary phloem or have been released from large compound sclereids by the disrupting forces of maceration.

Strands of aggregated sclereids, at least in many cases, are infrequent

or absent, even in much enlarged roots of this category of pereskias, and commonly do not occur in young stems. Thus, I suspect that such pereskias as *Pereskia bahiensis* Gürke and *P. moorei* Britt. & Rose, which have very large, relatively thin, characteristically pinnately veined leaves, will ultimately prove to belong in this category of species when adequate material of the largest and oldest stems can be obtained and studied.

3. Species with Ordinary "Stone Cells" Aggregated in Massive Irregular Clusters

In both the secondary phloem and cortex of older stems and roots of *Pereskia colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose, and *P. portulacifolia* Haw., simple, comparatively small sclereids occur in more or less massive aggregations of irregular form (PLATE IV). As indicated in longitudinal sections (FIG. 11), these aggregations do not have a consistently elongated form oriented parallel to the long axis of the stem or root. Furthermore, the sclerotic masses do not contain large compound sclereids but are composed of ordinary "stone cells" as regards size and form. These typical "stone cells" have profusely pitted, thick, lignified, multilayered walls (FIGS. 24–26). When they have a conspicuous major axis (FIG. 26), it tends to be oriented at right angles to, rather than parallel with, the long axis of the stem or root. It is evident from a developmental point of view that these sclereids differentiate from parenchymatous elements of the cortex and secondary phloem without excessive expansion and without internal septation.

DISCUSSION AND CONCLUSIONS

The occurrence of various forms of sclereids in the secondary phloem of pereskias and the absence of such cells in comparable tissue of *Pereskiopsis* and *Quiabentia* are obviously of some significance from a generic point of view, and parallel the presence or absence of glochids in these leaf-bearing genera. However, such differences must ultimately be considered in relation to close similarities that occur in other cells, tissues, and parts of the plants. Obviously a synthesizing discussion should be deferred to the last paper of this review.

The consistent differences in the form and distribution of sclereids in three distinct categories of pereskias are of considerable taxonomic significance, not only in the discussion of putative genera, e.g., *Rhodocactus*, but also in dealing with putative species and varieties. Evidence from the first category of pereskias is indicative of relationship of *Pereskia aculeata* to *P. diaz-romeroama* and *P. weberiana*, of Bolivia, and likewise to *P. conzattii*, of Southern Mexico, and *P. autumnalis* and *P. nicoyana*, of Central America. Evidence from the second category of pereskias is indicative of affinities between *P. sacharosa*, *P. grandifolia*, *P. bleo*, *P. corrugata*, and *P. tampicana*; that from the third category of pereskias of affinities between *P. colombiana* and *P. guamacho*, of northern South

America, and the West Indian endemics *P. cubensis* and *P. portulacifolia*.

The elongated or prosenchymatous form of the sclerenchymatous elements in the first category of pereskias raises the question whether the cells should be classified as phloem fibers with lignified, multilayered secondary walls or as elongated forms of sclereids. The occurrence of "ramifying" or coalescing simple pits in the thick secondary walls of these cells is a characteristic feature of many sclereids rather than of typical fibers. Furthermore, there are numerous transitions between short and variously elongated sclereids in the second category of pereskias. Admittedly, it is difficult to classify plant cells in rigid compartments, owing to the frequent occurrence of intergrading or transitional forms of morphological characteristics. However, in view of the well-known diversities in the size and form of sclereids (see Foster [5]) I am inclined to refer to more or less elongated cells in *Pereskia* having thick, lignified, multilayered walls with "ramiform" or coalescing pits as elongated forms of sclereids rather than as fibers.

The frequent occurrence of sclereids within fibers of the primary phloem and the formation of successive generations of smaller sclereids within large ones of the secondary phloem provide significant material for physiological and developmental investigations, as well as electron microscopy.

ACKNOWLEDGMENTS

EXPLANATION OF PLATES

PLATE I

FIGS. 1–3. DIFFUSE DISTRIBUTION OF SCLEREIDS IN TRANSVERSE SECTIONS OF STEMS. 1, *Pereskia aculeata* [Aw 9912] cluster of primary phloem fibers at A, a sclereid in the cortex at B, × 80. 2, *P. nicoyana* [*Rodriguez 662*], × 80. 3. *P. diaz-romeroana* [*Cárdenas*], × 80.

[5] Foster, A. S. Practical plant anatomy. Ed. 2. D. Van Nostrand Co., N. Y., 1949.

PLATE II

FIGS. 4–6. FREE AND INCLUDED SCLEREIDS. 4, *Pereskia nicoyana* [*Rodriguez 662*], longitudinal section of a stem showing elongated diffusely distributed sclereids in the secondary phloem, × 80. 5, *P. aculeata* [Aw 9912], transverse section of a sclereid in polarized light between crossed nicols, × 260. 6, Transverse section of septate fibers with included sclereids photographed in polarized light between crossed nicols, × 1200.

PLATE III

FIGS. 7–9. AGGREGATED SCLEREIDS OF THE SECOND CATEGORY OF PERESKIAS. 7, *Pereskia grandifolia* [*Castellanos*], transverse section showing two aggregations of sclereids in the secondary phloem, primary phloem fibers at A, × 80. 8, *P. sacharosa* [Tucumán], transverse section of a stem showing aggregation of sclereids in the secondary phloem, × 80. 9, *P. grandifolia* [*Castellanos*], longitudinal section of the secondary phloem showing elongated aggregation of sclereids, × 80.

PLATE IV

FIGS. 10–11. AGGREGATIONS OF "STONE CELLS" IN THE THIRD CATEGORY OF PERESKIAS. 10, *Pereskia cubensis* [Atkins Garden], transverse section of a root showing massive clusters of sclereids in the secondary phloem, × 80. 11, *P. guamacho* [*Steyermark*], longitudinal section of a stem showing irregular masses of sclereids in the outer secondary phloem and cortex, × 80.

PLATE V

FIGS. 12–17. DIAGRAMMATIC ILLUSTRATIONS OF PRIMARY PHLOEM FIBERS AND SCLEREIDS. Included protoplasts are stippled, primary walls and septa are black, first-formed secondary walls of fibers are white, and the secondary walls of sclereids are multilayered. 12, Characteristic form of immature primary phloem fibers prior to secondary wall formation. 13, Part of a nonseptate fiber having thick secondary wall and reduced lumen. 14, Part of a septate fiber having a relatively thin secondary wall. 15, Part of a septate fiber with included sclereids. 16, Precocious septation of an elongated cell prior to the formation of strand sclereids shown in Fig. 17.

PLATE VI

FIGS. 18–26. DIAGRAMMATIC ILLUSTRATION OF THE FORMS OF SCLEREIDS IN THREE CATEGORIES OF PERESKIAS. Included protoplasts are stippled, primary walls and septa are black, and the secondary walls of sclereids are multilayered. 18, Form of elongated, nonseptate sclereids in the first category of pereskias. 19, Part of the secondary wall of such a sclereid showing "ramiform" or coalescing pits. 20, Single, nonseptate sclereid from an aggregation in the second category of pereskias. 21, Compound sclereid from the same source showing three septa and four included smaller sclereids. 22, Doubly compound sclereid from the same source showing septation of such included sclereids as illustrated in Fig. 21 and the maturation of a second set of still smaller included sclereids. 23, Small laterally deformed sclereid. 24–26, Typical "stone cells" from aggregations in the third category of pereskias.
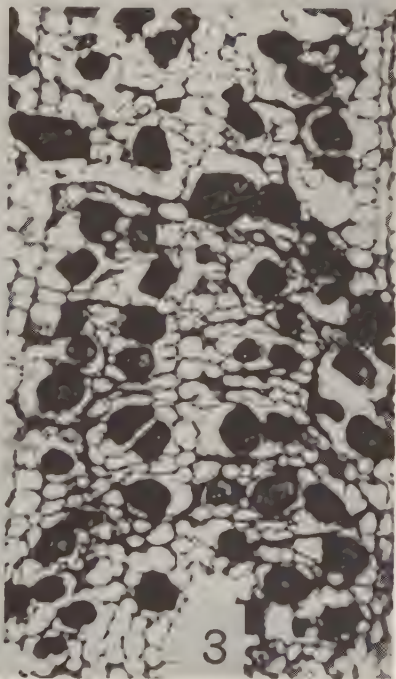
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II
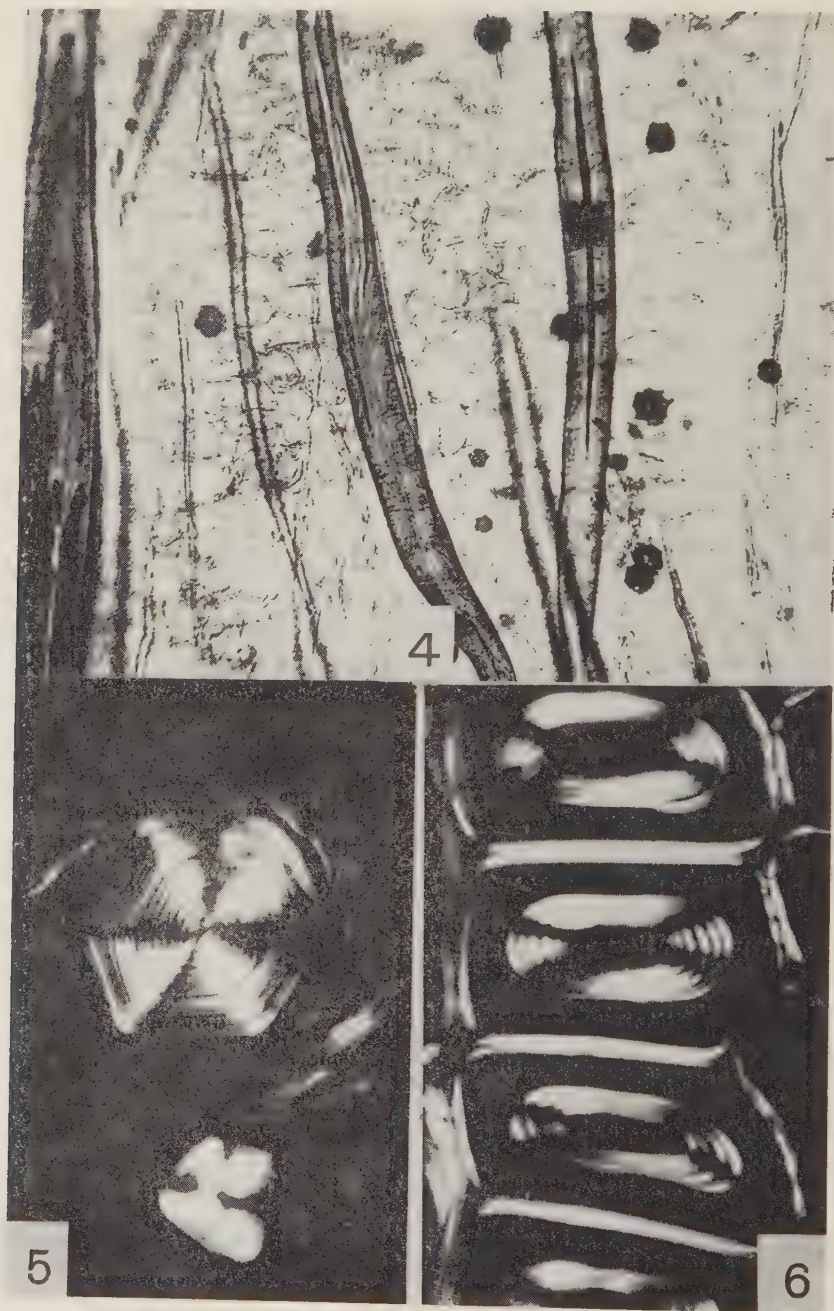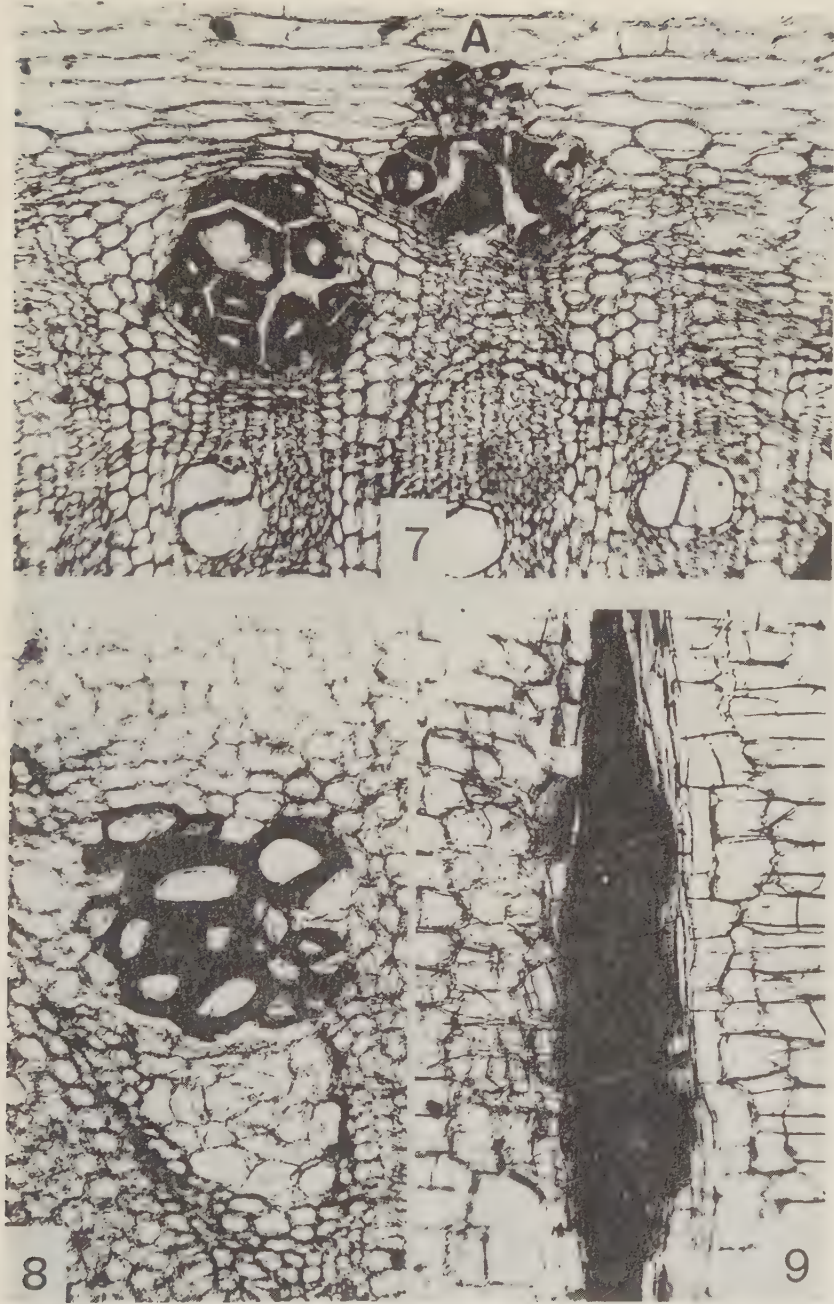
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II

Plate III

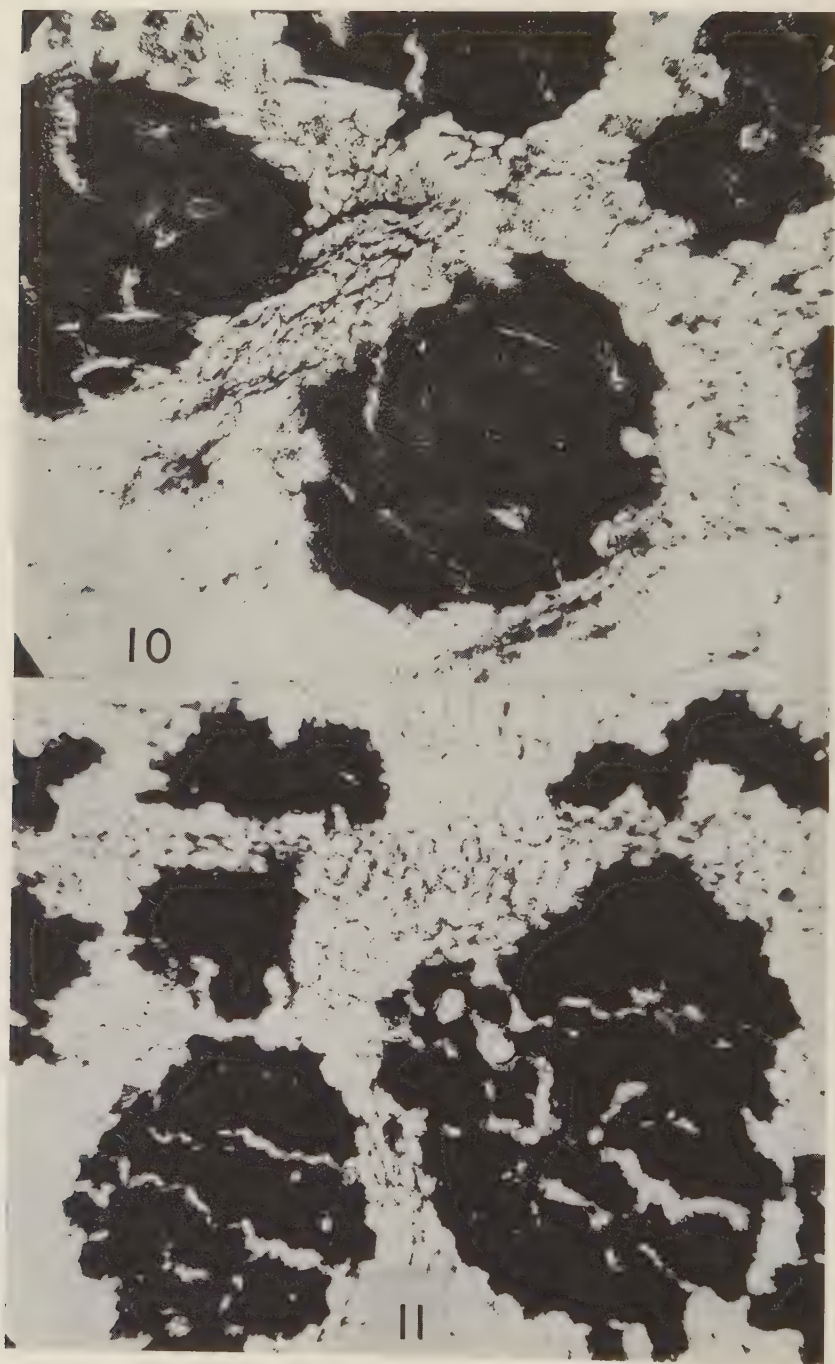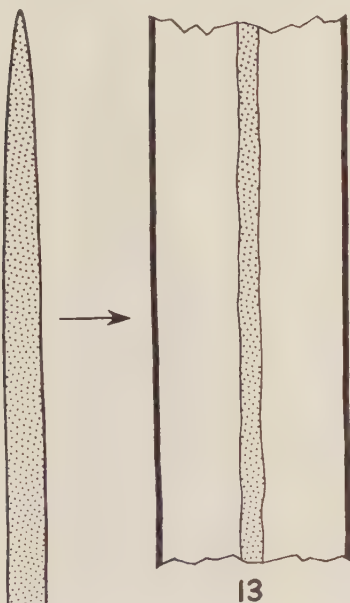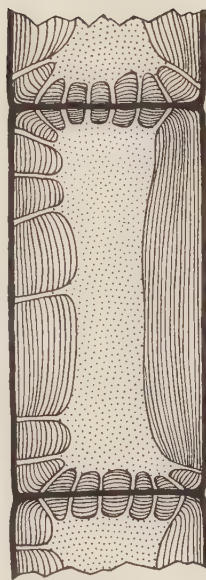BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II

10

11

BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II
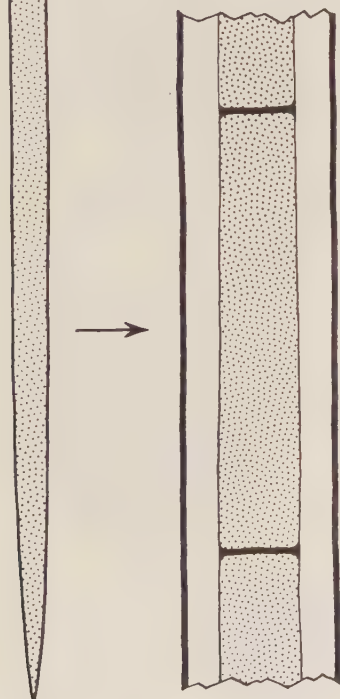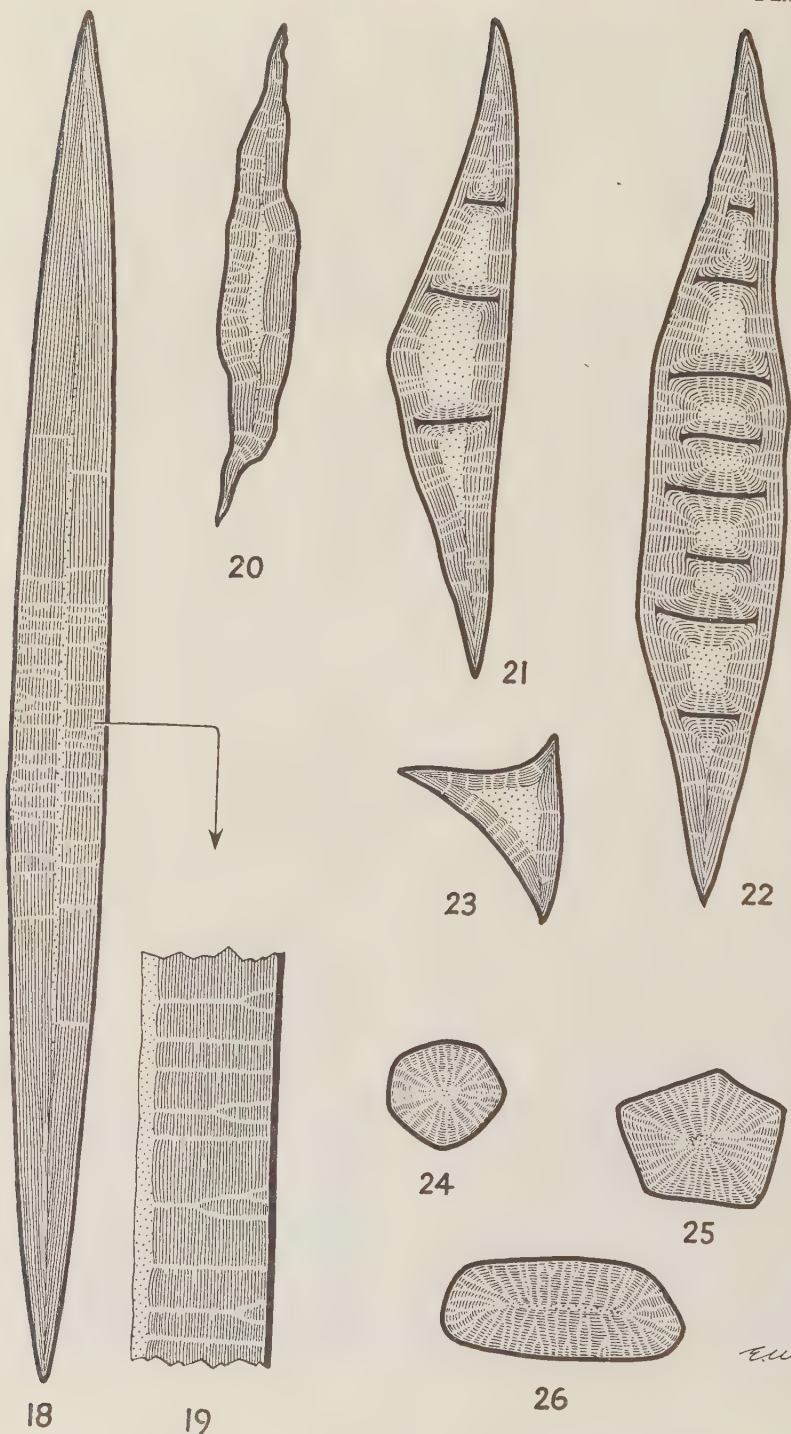
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, II

PLATE VI

THE CYTOLOGY OF SOME CULTIVATED
SPECIES OF VIBURNUM

Joab L. Thomas

Viburnum has long been recognized as a difficult group taxonomically, and more recently it has been shown to be somewhat complex cytologically. In recent years evidence from cytological studies has been used extensively in formulating taxonomic conclusions, but all too often only a small percentage of the species in a genus is studied cytologically, and, on the basis of these, generalizations are made concerning the entire genus. This has led to erroneous conclusions, both in cytology and taxonomy. It is hoped that additional studies in *Viburnum* will lead to a better understanding of the cytology of the genus, and that this, in turn, can be used in developing a sound and workable taxonomy.

The first chromosome counts in *Viburnum* were published in 1930 by Sax and Kribs (5) in a study of the cytology and wood structure in the Caprifoliaceae. In this paper chromosome numbers were reported for eleven species of *Viburnum* representing six of the nine sections of the genus, according to the classification of Rehder (3), and including both Asiatic and American species. All of the species included in this study were found to have nine pairs of chromosomes. However, in 1932, Simonet and Miedzyrzecki (6) reported that *Viburnum fragrans* has only eight pairs of chromosomes and, in 1936, Sugiura (7) reported that *V. awabuki* (*V. odoratissima*) has ten pairs of chromosomes. The most comprehensive study of the chromosomes of *Viburnum* was that of Janaki Ammal (1) in which a survey was made of the species growing in the botanical gardens at Wisley, Kew, and Paris. In this paper, chromosome counts were reported for the first time for twenty-three species and varieties, and additional counts were given for sixteen species for which counts had been reported previously by other authors. The present study was undertaken to extend the survey of chromosome numbers in *Viburnum* and to see if further evidence could be obtained on the origin of the aneuploid series in the genus. The chromosome counts obtained in this study, along with all other counts for *Viburnum* which I have seen, are listed in TABLE I. The classification used in this table is based on that of Rehder (4).

MATERIALS AND METHODS

The plant materials used in this study were from the living collection on the grounds of the Arnold Arboretum. Most of the chromosome counts were made from acetocarmine squashes of pollen mother cells. Satisfactory preparations were obtained by squashing fresh, whole anthers on a dry

TABLE I. **Chromosome Counts in Viburnum.**

SPECIES	2n	AUTHORITY *	DOCUMENTATION †	DISTRIBUTION
Sect. THYRSOSMA				
V. erubescens Wall.	48	1	none	Himal., w. China
V. foetens Decne.	16	1	none	Himal., Kashmir
V. fragrans Bunge	16	1, 6	none	n. China
var. *candidissima*	16	8	55–50–B	cult.
var. *alba*	32	1	none	n. China
V. grandiflorum Wall.	16	1	none	Himal.
V. henryi Hemsl.	48	1	none	centr. China
V. odoratissimum Ker-Gawl.	40	1	none	India, China
V. seiboldii Miq.	16	1	none	Japan
"	32	8	AA616–6–B	"
V. suspensum Lindl.	16	1	none	Liukiu Islands
Sect. LANTANA				
V. bitchiuense Makino	16	1	none	w. Japan
V. buddleifolium Wright	20	1	none	centr. China
"	18	6	none	"
V. × *burkwoodii* Burkwood & Skipwith (*V. carlesii* × *utile*)	18	8	AA815–41–B	cult.
V. × *carlcephalum* Burkwood ex. Pike (*V. carlesii* × *macrocephalum*)	18	8	AA618–53–A	cult.
V. carlesii Hemsl.	20	1	none	Korea
"	18	2, 6, 8	AA17981–A	"
V. cotinifolium D. Don	18	2	none	Himal.
V. lantana L.	18	1, 2, 5	none	Eur., w. Asia
var. *rugosum* Lange	18	8	AA907–27–A	cult.
V. mongolicum (Pall.) Rehd.	16	1	none	e. Siberia, n. China
V. × *rhytidophylloides* Suringar (*V. rhytidophyllum* × *lantana*)	18	8	AA711–36–B	cult.
V. rhytidophyllum Hemsl.	18	1, 6	none	centr. & w. China
V. utile Hemsl.	18	1	none	centr. China
V. urceolatum Seib. & Zucc.	18	8	AA876–51	Japan
V. veitchii Wright	18	8	AA7198	centr. China
Sect. PSEUDOTINUS				
V. alnifolium Marsh.	18	1, 5	none	e. N. Am.
V. furcatum Blume ex Maxim.	18	1	none	Japan
Sect. PSEUDOPULUS				
V. plicatum Thunb.	16	8	AA18016–1	Japan, China
f. *lanceatum* Rehd.	16	8	AA6122–1	cult.
f. *mariesii* (Veitch) Rehd.	18	8	AA870–51–A	cult.
f. *roseum* (Doney) Rehd.	16	8	AA856–34	cult.

TABLE I (*Continued*)

SPECIES	2n	AUTHORITY *	DOCUMENTATION †	DISTRIBUTION
Sect. LENTAGO				
V. cassinoides L.	18	8	AA17997	e. N. Am.
V. lentago L.	18	1, 5	none	e. N. Am.
V. nudum L.	18	1	none	e. N. Am.
V. prunifolium L.	18	1, 5	none	e. N. Am.
Sect. TINUS				
V. cinnamomifolium Rehd.	18	1	none	w. China
V. davidii Franch.	18	1	none	w. China
V. harryanum Rehd.	18	2	none	w. China
V. propinquum Hemsl.	18	2	none	centr. & w. China
V. tinus L.	36	1, 2, 6	none	se. Eur.
Sect. ODONTOTINUS				
V. acerifolium L.	18	1, 5	none	e. N. Am.
V. betulifolium Batalin	18	1	none	centr. & w. China
V. dentatum L.	54	1	none	e. N. Am.
"	36	8	AA17985	"
var. *pubescens* Ait.	36	8	AA18009	"
V. dilatatum Thunb.	18	8	AA229–46–B	e. Asia
f. *hispidum*	18	8	AA17486–1–A	cult.
f. *xanthocarpum* Rehd.	18	8	AA10140	cult.
V. foetidum Wall. var. *rectangulatum* (Graebn.) Rehd.	16	1	none	w. China
	16	1	none	w. China
V. hirtulum Rehd.	18	8	AA708–37–B	China
V. hupehense Rehd.	18	5, 6	none	China
V. lobophyllum Graebn.	20, 22	1	none	centr. & w. China
"	18	5	none	"
V. molle Michx. f. *leiophyllum* Rehd.	18	8	AA4643–1–A	e. N. Am.
V. ovatifolium Rehd.	18	1, 8	AA20078A	w. China
V. pubescens Pursh	36	8	AA18008	e. N. Am.
V. raffinesquianum Roem. & Schult. var. *affine* (Schneid.) House	20	8	AA4622–2–B	e. N. Am.
V. setigerum Hance	36	8	AA20189	centr. & w. China
" (as *V. theiferum* Rehd.)	18	6	none	"
f. *aurantiacum* Rehd.	36	8	AA812–32	"
V. wrightii Miq.	16	1	none	Japan
Sect. OPULUS				
V. opulus L.	18	1, 5	none	Eur. & n. Africa
f. *xanthocarpum* (Endl.) Rehd.	18	8	AA1298–28–A	cult.
V. sargentii Koehne	18	5	none	ne. Asia
f. *calvescens* (Rehd.) Rehd.	18	8	AA467–26	cult.
V. trilobum Marsh.	18	1, 5	none	n. N. America
'compactum'	18	8	AA871–51	cult.

* 1, Janaki Ammal; 2, Poucques; 5, Sax; 6, Simonet and Miedzyrzecki; 7, Sugiura; 8, Thomas, reported here for the first time.

† The numbers listed under this column are the accession numbers for the plants in the living collection of the Arnold Arboretum. Voucher specimens of these plants bearing the accession number have been deposited in the herbarium of the Arnold Arboretum.
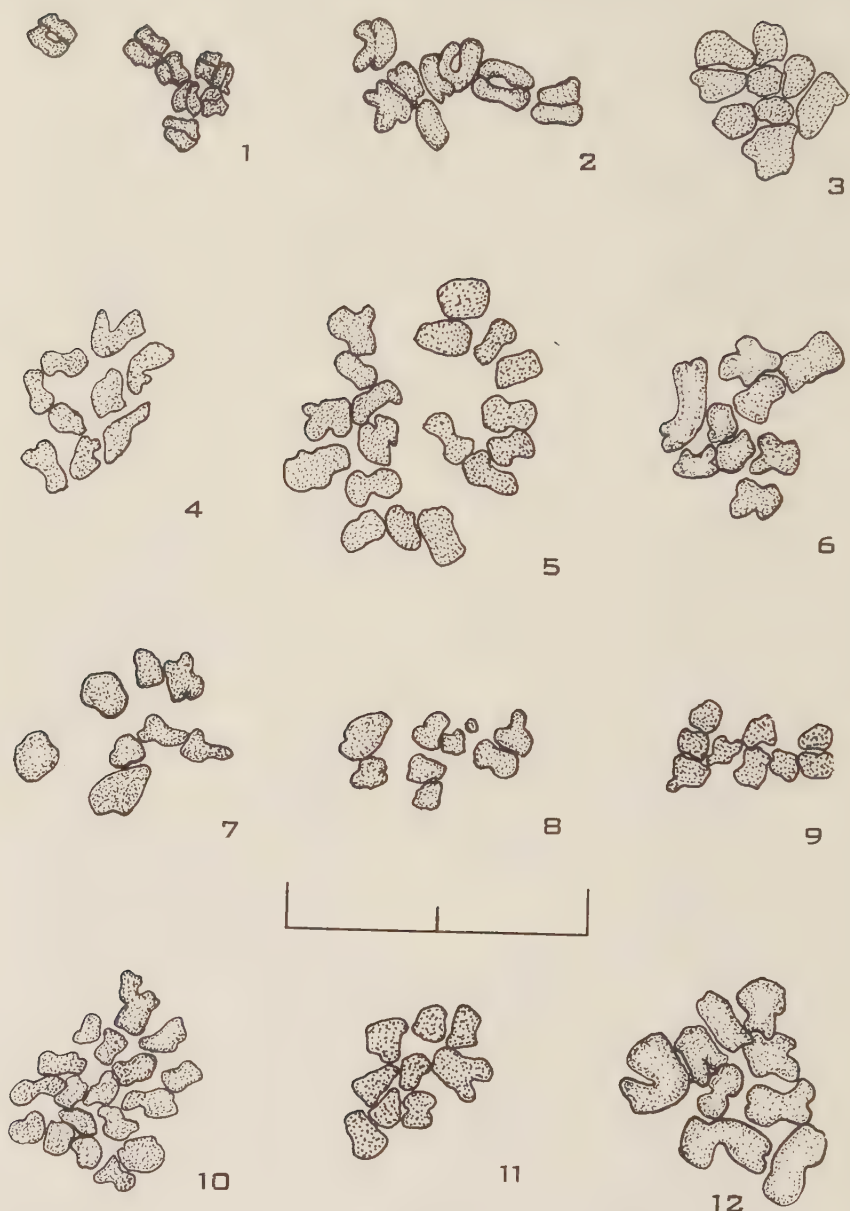
FIGS. 1–12. CHROMOSOMES OF VIBURNUM. 1, *V. fragrans* var. *candidissima*, metaphase II; 2, *V. carlesii*, late metaphase I; 3, *V. ovatifolium*, metaphase I; 4, *V. rhytidophylloides*, telophase II; 5, *V. pubescens*, metaphase I; 6, *V. veitchii*, metaphase I; 7, *V. plicatum*, metaphase I; 8, *V. plicatum* f. *mariesii*, metaphase I; 9, *V. dilatatum* f. *hispidum*, metaphase II; 10, *V. dentatum*, metaphase I; 11, *V. dilatatum* f. *xanthocarpum*, metaphase II; 12, *V. opulus* f. *xanthocarpum*, metaphase I. Each division in the scale represents 10 micra.
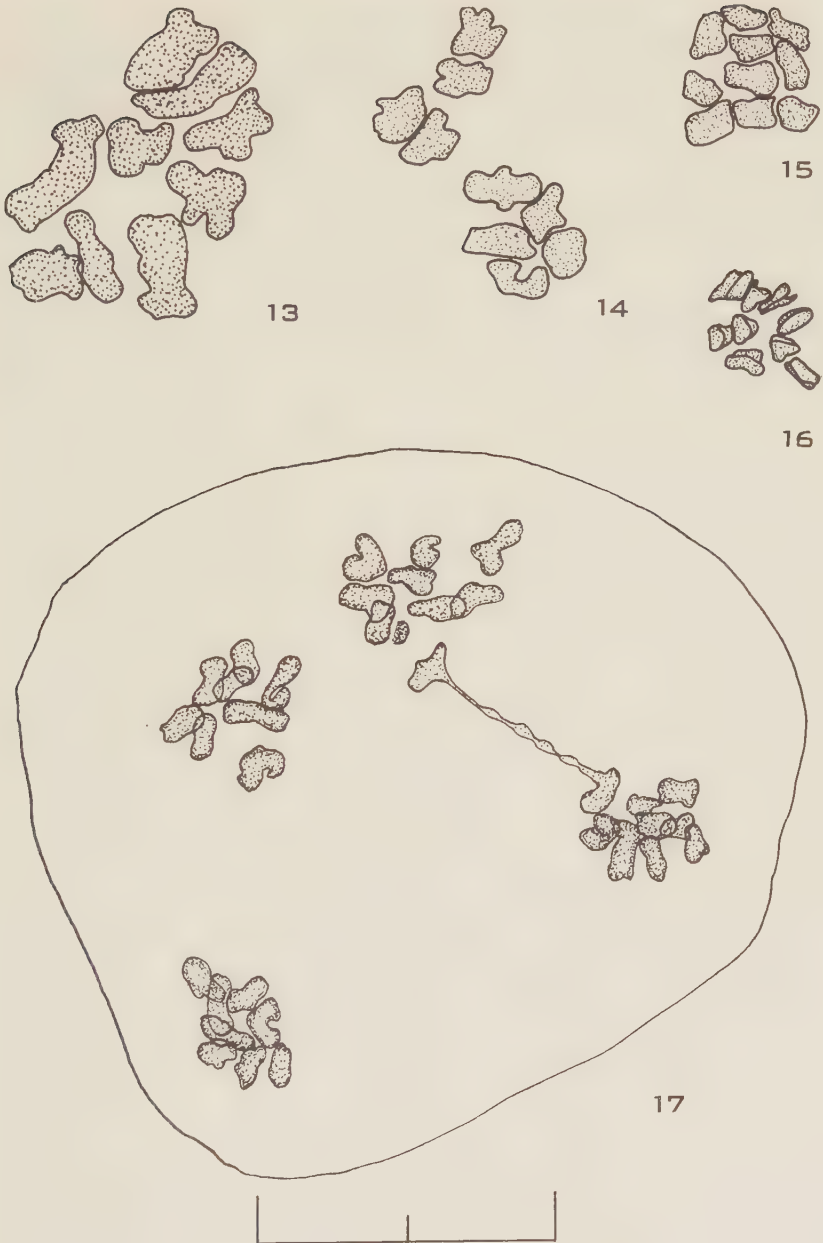
FIGS. 13–17. CHROMOSOMES OF VIBURNUM. 13, *V. cassinoides*, metaphase I; 14, *V. urceolatum*, metaphase I; 15, *V. rafinesquianum* var. *affine*, metaphase I; 16, *V. lantana* var. *rugosum*, metaphase II; 17, *V. rhytidophylloides*, telophase II, showing loss of a chromosome due to unequal translocation. Each division in the scale represents 10 micra.

slide, immersing the slide in Carnoy's fixative for ten to twenty minutes, and staining the material with acetocarmine. In a few cases, counts were made on root tips obtained from rooted cuttings. The root tips were treated for two to three hours in 0.1% colchicine, fixed in Carnoy's solution, softened in concentrated HCl for ten to fifteen minutes, and stained with acetocarmine.

The time of flowering varies considerably in different species of *Viburnum*, and meiosis often occurs over a short period of time. In order to avoid missing meiosis in several species, small cuttings were brought indoors and forced. Most species forced readily after the middle of March and it was much easier to follow their development under the relatively uniform conditions in the laboratory, than under the highly variable spring weather conditions outside.

ORIGIN OF THE ANEUPLOID SERIES

Janaki Ammal (1) has postulated the origin of the chromosome numbers nine and ten starting with a base number of eight for the genus. The number ten was thought to have originated from a backcross between a chance triploid ($2n = 24$) and a diploid ($2n = 16$) to produce $2n = 20$. Plants with this number are referred to as "secondary diploids." The number nine was said to have originated from hybridization between plants having $2n = 20$ and $2n = 16$, and are referred to as "tertiary diploids." The origin of *Viburnum juddii* was cited as an example of the latter.

This explanation is very logical and it is possible that some species of *Viburnum* have originated in this manner. However, in view of the evidence at hand it seems more likely that species with chromosome numbers of eight and ten originated from species with a base number of nine by the gain or loss of a chromosome. The base number nine is by far the dominant number in the Caprifoliaceae, as well as in the genus *Viburnum*. Of the 50 species of *Viburnum* for which chromosome counts are available (not including varieties, forms, or cultivars) twelve have a base number of eight, 33 have nine, and only two have undisputed counts of $x = 10$. Three additional species were reported by some workers to have $x = 10$ but by other workers to have $x = 9$. It seems probable that the discrepancies here are due to real differences in the chromosome numbers of the plants counted, rather than to mistakes in counting. There are no discrepancies reported for species with $x = 8$, whereas three of the five species reported to have $x = 10$ also have reported counts of nine, and one of these also has a count of eleven. Thus, the number ten seems to be relatively unstable, which is what one would expect if it originated by the gain of a chromosome from species with nine. The duplicated chromosome material is apparently lost with little or no deleterious effect on the plant.

Among the species in which there is a discrepancy in the reported chromosome numbers *Viburnum carlesii* is particularly significant. As mentioned above, Janaki Ammal used the case of *V. juddii* to illustrate the origin of the nine-chromosome series. *Viburnum juddii* is an open-

pollinated offspring of *V. carlesii*, with *V. bitchiuense* suggested as the most probable male parent. The chromosome counts reported for these plants by the above author were as follows: *V. carlesii*, $2n = 20$; *V. bitchiuense*, $2n = 16$; and *V. juddii*, $2n = 18$. However, Poucques (2) and Simonet and Miedzyrzecki (6) reported counts of $2n = 18$ for *V. carlesii*, and, upon checking the original plant from which *V. juddii* originated, I found that it, too, has $2n = 18$. It is fortunate, indeed, that the original plant is still growing on the grounds of the Arboretum and that thorough records were kept documenting the female parent of this hybrid species. I have not yet examined the plants of *Viburnum bitchiuense* which are growing in the vicinity of *V. carlesii*, but if they do have a chromosome number of $2n = 16$, as reported, it seems highly unlikely that this species served as the male parent of *V. juddii*.

Chromosome aberrations were fairly common in several of the species of *Viburnum* which I examined, and unequal divisions were noted in several instances. Translocations apparently occurred rather frequently as evidenced by bridge formations observed in several of the species (see FIG. 17). A relatively high percentage of aberrations was noted in *Viburnum cassinoides*, *V. carlcephalum*, *V. carlesii*, *V. dentatum*, *V. plicatum*, *V. rhytidophylloides*, *V. seiboldii*, *V. trilobum* f. *compactum*, and *V. veitchii*.

In a situation such as this the opportunities for gaining or losing a chromosome are greatly increased, and with frequent translocations the chances of losing a chromosome and still retaining a viable chromosome complement are also increased. An example of the gain of a chromosome is that of *Viburnum plicatum* f. *mariesii*, which originated in cultivation. *Viburnum plicatum* and two of its cultivated forms, f. *lanceatum* and f. *roseum* have $2n = 16$, whereas f. *mariesii* has an extra pair of chromosomes which are very small but nevertheless apparently pair and divide normally during meiosis.

Viburnum is still in need of further cytological work to give a more complete picture of the natural distribution of the three chromosome series. Less than half of the species have been studied cytologically, these being cultivated species, for the most part, and, in many cases, species that have been in cultivation for a long time. Additional cytological work, well documented with herbarium specimens, is needed particularly on Asiatic species from the wild.

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MIOCENE FOSSIL WOODS FROM THE COLUMBIA BASALTS OF CENTRAL WASHINGTON

U. Prakash and Elso S. Barghoorn

Over extensive areas of the northwestern United States, especially in Central Washington, there occur thick accumulations of basalt and related pyroclastic sediments. These are known as the Columbia Lava Series and contain within them numerous fossil woods, in places preserved virtually as fossil forests *in situ*. One of the areas most extensively investigated has been designated locally as the Russell Forests, the term proposed by Beck (1945a). The area included under this designation comprises several hundred square miles in an area centered around Vantage, in the Columbia Valley. Beck (1955–1956) noted that in botanical composition and age, the fossil forests are quite comparable in botanical identity, on the generic level, with the well-known leaf impressions from the Latah beds in and around the city of Spokane, Washington. In Beck's extensive studies, he listed (1945a) thirteen localities in which fossil woods had been found in varying abundance.

In a series of informal notes and publications, Beck presented an impressive list of identified fossil dicotyledonous and coniferous woods (Beck 1941a–e; 1942a–c; 1942–43; 1944a–c; 1945a–c; 1948; 1955a–c; 1955–56; 1956). Unfortunately, however, the identifications are, with few exceptions, not associated with illustration, anatomical description and formal binomial designation. Hence, they do not constitute permanent accessible additions to palaeobotanical and palaeogeographic literature. The authors are in full agreement with the validity and accuracy of Beck's investigations on the fossil woods of central Washington and wish to dedicate this study, in part, to commemoration and formalization of his many years of painstaking work in this difficult aspect of palaeobotanical research. The genera and species described in this paper comprise only a fraction of those which have been determined from the Columbia Basalt fossil forests, and it is proposed to expand our taxonomic treatment of this flora as additional material is examined.

The locality of particular interest is near the town of Vantage, Kittitas County, Washington, on the west bank of the Columbia River about 28 miles east of Ellensburg. From Beck's study (1945a) and our own observations, it is evident that the Vantage locality is rich in quantity and diversity of fossil woods. It is of much interest also to note that this region, once covered by a rich deciduous forest, is now featured by a semiarid sagebrush vegetation (*Artemisia*). The various causes for extinction of the forest, the pronounced changes in climate and topography of the region and other related problems will be dealt with in a subsequent paper when the flora and its ecological significance are more fully known.

This paper deals with the systematic description of woods belonging to the families Aceraceae, Ebenaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Leguminosae, Platanaceae, and Ulmaceae. The field collection was made in 1954 by Mr. Jay O'Leary while he was a student in Harvard College. Our determinations are based on his specimens and preparations supplemented by additional thin-sections.

In general, the preservation of structural details of the wood is quite good, although not consistently so. The siliceous matrix fluctuates from hyaline to microcrystalline but is not accompanied, to any serious degree, by opaque minerals. Some specimens are varicolored by iron mineral stain, but even in these cases the woody structure is well preserved.

The age of the fossil woods described in this study is Upper Miocene. This determination is consistent with the presently accepted stratigraphic position of the Columbia basalts in this area of Washington.

ACERACEAE

1. **Acer puratanum** Prakash & Barghoorn, sp. nov. (FIGS. 25–28, 30)

Growth rings: Fairly distinct (FIG. 27), delimited by 2 or 3 rows of thick-walled fibers.

Vessels: Small, 30–72μ in tangential diameter (mean 53μ); chiefly solitary (FIG. 27), often in multiples of 2–several cells, quite uniform in size and evenly distributed, thin-walled, the solitary vessels round to oval in cross-section. Vessel elements 130–350μ long, with spiral thickenings (FIG. 26). Perforation plates exclusively simple, oblique, often tailed. Intervascular pit-pairs bordered (FIG. 30), alternate, orbicular or angular where crowded, 5–7μ in diameter, with linear apertures. Tyloses absent; vessels often plugged with yellow or brown gummy deposits.

Parenchyma: Sparse, restricted to occasional cells; terminal and paratracheal. Terminal parenchyma occurring as scattered cells associated with the narrow terminal bands of thick-walled fibers. Paratracheal parenchyma (FIG. 25) scanty, occurring as a few cells in association with the vessels. Parenchyma cells sometimes crystalliferous.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed chiefly of procumbent cells (FIG. 28), nonstoried, 1–5 cells wide; uniseriate rays quite common, 1–15 (often 3–8) cells high; multiseriate rays mostly 3–4 cells broad and 0.56 mm. high; up to 8–12 rays per mm. Ray cells square, rectangular or oval in tangential section, thin- to moderately thick-walled and 10–20μ in diameter.

Imperforate tracheary elements: Fiber tracheids (FIG. 25) thin- to moderately thick-walled, especially through the late-wood zone near the growth ring, usually polygonal in cross-section with a small to large lumen, 8–20μ in diameter, nonseptate; pits bordered.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 4 $\times$ 4 $\times$ 3 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55200. The name is derived from Sanskrit, *puratan*, meaning *ancient*.

There is close agreement in almost all details of structure of this wood with that of *Acer*. The fossil wood shows also a superficial resemblance to the mature secondary xylem of *Betula* as seen in transverse and tangential sections. However, in *Betula*, the perforation plates are scalariform, in contrast with the simple plates in *Acer*. Also, spiral thickenings are present in the vessels of *Acer* but absent in *Betula*. A survey of available woods of *Acer* indicates that the nearest affinity of the fossil within this genus is with *A. circinatum* Pursh and *A. mandschuricum* Maxim., especially with the former. Our survey included the study of thin-sections of the woods of 29 species of the genus and published descriptions of 14 other species. The latter are *A. oblongum* Wall., *A. caesium* Wall., *A. thomsonii* Miq. (Pearson and Brown, 1932, pp. 299–308, *figs. 107–111*), *A. pseudoplatanus* L. (Kribs, 1959, *fig. 61*), *A. cissifolium* C. Koch., *A. rufinerve* Sieb. & Zucc. (Kanehira, 1921a, pp. 17, 18), *A. rubescens* Hay., *A. kawakamii* Koidz., *A. duplicato-serratum* Hay., *A. oliverianum* Pax var. *nakaharai* Hay., *A. taiton-montanum* Hay., *A. morrisonense* Hay. (Kanehira, 1921b, pp. 74–76, *pl. 14, figs. 79–81*), *Acer circinatum* Pursh, and *A. leucoderme* Small (Stark, 1954, pp. 8, 10).

The size and distribution of the vessels in *Acer puratanum* agree with the distributional pattern in *A. circinatum*. Tangential diameter of vessels in *A. puratanum* ($30–72\mu$) is quite comparable to the measurements secured from comparable secondary xylem of *A. circinatum* ($25–72\mu$). Both in *A. circinatum* and in the fossil species the perforations are simple and the intervascular pit-pairs are alternate, bordered, orbicular, or angular where crowded, with linear apertures. However, the vessels are more closely placed in the fossil wood than in the modern wood of *A. circinatum*.

The distribution of parenchyma appears to be almost identical in both, as is the fiber and ray structure. However, conspicuous differences between the two species are in the crystalliferous parenchyma and the distribution of thick-walled fibers. The crystalliferous parenchyma is occasionally present in the fossil wood but absent in *Acer circinatum*, although it is known to occur in a number of other species of *Acer*. Also, *A. circinatum* shows alternate areas of thin- and thick-walled fibers (Stark, 1954, p. 8), whereas in *A. puratanum* thick-walled fibers are found only in the late wood.

Fossil woods related to *Acer* are known from the Cretaceous onward under the names *Acerinum* Unger (1842), *Aceroxylon* Loubière (1939), and *Acer* L. These woods are *Acerinum danubiale* Unger (1842), from the Tertiary of Upper Austria; *A. borussicum* Caspary (1888) and *A. terraecoeruleae* Caspary (1888), from the Tertiary (?) of East Prussia; *A. aegypticum* Schenk (1888, 1890), from the Tertiary of Egypt; *A. astianum* Pampaloni (1904), from the Tertiary of the Piedmont; *Aceroxylon madagascariense*, from the Cretaceous of Madagascar (Loubière, 1939); *Aceroxylon* cf. *paleosaccharinum* Greguss (1943), from Hungary; *Aceroxylon* sp., from the Oligocene of Prambachkirchen, Austria (Hofmann, 1944, 1952); *Acer* sp. (Szafer, 1914; Fietz, 1926b), from the Pleistocene of Poland, and from the prehistoric deposits of Czechoslovakia; *Acer iwatense*

Watari (1941, 1952) and *Acer* cf. *amoenum* Carr. (Watari, 1952), from the Tertiary of Japan. However, our present fossil wood differs distinctly from all the known species. Thus, *Acer* cf. *amoenum* (Watari, 1952) differs from *A. puratanum* in having broad xylem rays 1–9 cells wide and in the presence of diffuse parenchyma in addition to paratracheal and terminal types. Diffuse parenchyma is absent from *A. puratanum*. Similarly, *A. iwatense* (Watari, 1941, 1952) also differs from *A. puratanum* in having broad, homogeneous to heterogeneous xylem rays, 1–7 cells wide, and in the presence of only diffuse parenchyma.

The family Aceraceae is composed of two genera and about 150 species. One genus, *Dipteronia*, comprises two species of small trees indigenous to China. The other, *Acer*, composed of numerous species of small to large deciduous trees, is widely distributed over the Northern Hemisphere, one form extending south of the equator to the mountains of Java. It attains its greatest development in eastern Asia and eastern North America (Record and Hess, 1943; Stark, 1954). There are only thirteen species of *Acer* indigenous to the United States. *Acer saccharum* Marsh. and *A. nigrum* Michx. occur in most of the eastern hardwood region of the United States and Canada and also locally in northeastern South Dakota, with the best stands near the Great Lakes and in northern New England and the St. Lawrence Valley (Munns, 1938, *maps 148, 149*; Record and Hess, 1943). *Acer saccharum* Marsh. also grows in southwestern Manitoba, eastern Oklahoma and northeastern Texas. The two principal soft maples, *A. rubrum* L. and *A. saccharinum* L., have much the same range, but extend farther south and attain their best development in the lowlands of the Ohio Valley (Munns, 1938, *maps 150, 151*). *Acer macrophyllum* Pursh grows along the Pacific Coast, from British Columbia to southern California, with the greatest development in Washington and Oregon (Munns, 1938, *map 147*). *Acer pennsylvanicum* L. (Munns, 1938, *map 146*) and *A. spicatum* Lam. grow in the undergrowth of the northeastern hardwood forests and also south in the mountains to northern Georgia (Record and Hess, 1943). *Acer circinatum* Pursh grows naturally along streams and lakes, often forming impenetrable thickets, from British Columbia to northern California, mainly near the coast (Britton, 1908, p. 642). *Acer negundo* L. ranges naturally from western Vermont to western New Jersey and central Florida, westward to Ontario, Manitoba, central Saskatchewan, southern Alberta, central Montana, Wyoming, Utah, California, and Mexico (Munns, 1938, *map 152*; Little, 1953). *Acer leucoderme* Small inhabits rocky river-banks and ravines from North Carolina and Georgia, westward to southeastern Oklahoma and Louisiana. *Acer grandidentatum* Nutt. is a species of the Rocky Mountain region and ranges from northern Montana to eastern Utah, Wyoming, western Texas, and New Mexico, extending southward into Mexico. *Acer barbatum* Michx. (*A. floridanum* (Chapm.) Pax) grows naturally from southeastern Virginia to central Florida and is reported to exist farther west in Texas, northern Mexico, and north in the Mississippi Valley to southeastern Missouri. *Acer glabrum* Torrey grows from Montana, southwestern Oregon, and Idaho to Wyoming,

western Nebraska, and throughout Colorado to New Mexico and Arizona, and also the Sierra Nevada of California (Britton, 1908, pp. 640–56; Little, 1953).

2. **Acer beckianum** Prakash & Barghoorn, sp. nov. (FIGS. 59–63)

Growth rings: Distinct, delimited by 1 or 2 layers of flattened thick-walled fibers.

Vessels: Small, 30.6–81.5μ in tangential diameter (mean diameter 60μ), chiefly solitary (FIG. 62), sometimes in multiples of 2 or 3 or rarely 4 or 5 cells, uniform in size and evenly distributed, slightly thick-walled, the solitary vessels round to oval in cross-section (FIGS 61, 62). Vessel segments 102–408μ long with spiral thickenings (FIG. 59); end walls usually oblique, sometimes horizontal and often tailed. Perforation plates exclusively simple. Intervascular pit-pairs (FIG. 60) bordered, alternate, 7–8μ in diameter, orbicular (or angular where crowded) with linear apertures. Tyloses absent; vessels sometimes plugged with brown or black gummy deposits.

Parenchyma: Sparse, terminal and paratracheal. Terminal parenchyma scanty, associated with the growth ring. Paratracheal parenchyma found as 1–few cells in association with some vessels.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1) composed chiefly of procumbent cells, nonstoried; 1–3 cells wide; uniseriate rays quite frequent, 3–16 cells high; multiseriate rays mostly 3 cells broad and 0.7 mm high; up to 12–16 rays per mm. Ray cells round to oval, sometimes vertically elongate in tangential section, thick-walled and 7–14μ in diameter.

Imperforate tracheary elements: Fiber tracheids polygonal in cross-section, 10–18μ in diameter, the walls thin to thick, with a small to large lumen, non-septate; pits bordered.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 4 × 2.5 × 3 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55226. The species is named in honor of George F. Beck, of Yakima, Washington, who pioneered the work on the fossil woods of Vantage and its neighboring areas.

A survey of all available woods of the genus *Acer* indicates that the nearest affinity of the fossil is with *Acer negundo* L. The size and distribution of the vessels of *A. beckianum* agree with the distributional pattern in *A. negundo* var. *violaceum* Jaeg. & Beissn. The tangential diameter of the vessels in the fossil wood (30.6–81.5μ) is somewhat similar to the measurements secured from comparable secondary xylem of *A. negundo* (25–80μ). The only obvious difference between the two species is in the shape of the vessels which are mostly oval and slightly angular in *A. negundo* but almost always round in *A. beckianum*.

The distribution of parenchyma appears to be almost identical in both,

as is the fiber and ray structure. However, a minor difference between the two species is in lower and rarely 4-seriate rays in *A. negundo*; the rays are slightly higher and up to 3-seriate in *A. beckianum*.

As previously noted, a number of fossil woods related to *Acer* are known and all of them differ from *Acer beckianum* in certain features. The fossil wood of *A. puratanum* Prakash & Barghoorn, described in the preceding pages and from the same locality, also differs distinctly from *A. beckianum*.

3. **Acer olearyi** Prakash & Barghoorn, sp. nov.   (FIGS. 55–58)

Growth rings: Slightly distinct, delineated by flattened, thick-walled fibers.

Vessels: Small, 30–80μ in tangential diameter (FIG. 55), (mean diameter 58.5μ); commonly in multiples of 2–8 cells, often solitary, almost uniform in size and evenly distributed, thin-walled, the solitary vessels round to oval or slightly angular in cross-section, radially compressed when in multiples. Vessel elements with spiral thickenings, the end walls probably oblique. Perforation plates exclusively simple. Intervascular pit-pairs bordered, alternate, slightly loosely arranged, 5–7μ in diameter, orbicular (or angular when crowded), with linear to lenticular apertures. Tyloses absent, but vessels commonly plugged with brown or black gummy deposits (FIG. 55).

Parenchyma: Scanty, terminal, paratracheal and diffuse. Terminal parenchyma occurs as occasional cells associated with the rows of thick-walled fibers at the growth ring. Paratracheal parenchyma very sparse, 1–few cells associated with the vessels, sometimes forming incomplete sheaths.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed of procumbent cells (FIG. 58), nonstoried, 1–7 cells wide; uniseriate rays common, 3–16 cells high; multiseriate rays mostly 5 or 6 cells broad and 1.05 mm. high; up to 8–10 rays per mm. Ray cells square, rectangular, or polygonal in tangential section and 8–15μ in diameter.

Imperforate tracheary elements: Fiber tracheids oval to angular in cross-section, 12–25μ in diameter, the wall thin to thick with a small to large lumen, non-septate; pits bordered.

MATERIAL. A single specimen of silicified, mature, secondary xylem measuring 3.5 $\times$ 4 $\times$ 2.5 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University No. 55311. This species is named for Mr. Jay O'Leary, who collected this material.

A survey of all available woods of the genus *Acer* indicates that the nearest affinity of the fossil is with *Acer grandidentatum* Nutt. Both in *Acer olearyi* and the modern wood of *A. grandidentatum* the vessel size and their distribution, the nature of the perforation plates, the intervascular pit-pairs, the parenchyma distribution, and the ray and fiber structure are similar. However, the only obvious difference between the two species is that the vessels are more crowded and with a slightly greater frequency of the vessel multiples in *A. grandidentatum* than in *A. olearyi*.

Acer grandidentatum Nutt. occurs in the western United States and ranges from northern Montana to eastern Utah, Wyoming, western Texas, and New Mexico, extending southward into Mexico (Britton, 1908, p. 652). The present fossil wood differs from all extant species examined as well as from the other fossil species described so far.

EBENACEAE

4. **Diospyros washingtoniana** Prakash & Barghoorn, sp. nov.

(Figs. 46–50)

Growth rings: Distinct; wood semi-ring-porous (Fig. 47).

Vessels: Large vessels in the early wood, gradually decreasing in size towards the outer margin of the ring (Fig. 47), 40–240μ in tangential diameter (mean diameter 146μ); sometimes solitary, usually in radial rows of 2–4 cells, evenly distributed and somewhat widely placed, thick-walled; solitary vessels round to oval or elliptical in cross-section (Figs. 47, 49), sometimes irregular in shape. Vessel elements 190–310μ long with horizontal to oblique end walls. Perforation plates exclusively simple. Intervascular pit-pairs bordered, minute, 3–5μ in diameter, orbicular to oval, with linear apertures, sometimes confluent. Vessels often plugged with black or brownish gummy deposits and tyloses (Fig. 50).

Parenchyma: Paratracheal, metatracheal, and terminal. Paratracheal parenchyma confined to immediate vicinity of the vessels, the sheath being narrow, 1- or 2-seriate but incomplete. Metatracheal parenchyma distinguishable with difficulty in cross-section because of bad preservation, but apparently quite abundant and arranged in broken, irregular tangential bands 1–3 cells thick, sometimes ending blindly. Terminal parenchyma forming a 1- or 2-seriate tangential band at the growth ring. Parenchyma cells usually larger than the fibers, variously shaped, those occurring in close association with the vessels flattened to conform to the vessel wall, those found elsewhere oval to rectangular in shape.

Xylem rays: Homogeneous to heterogeneous, storied (Fig. 48) but slightly irregular in some places, 1–2 (mostly 2)-seriate and 0.45 mm. high; uniseriate rays 2–13 cells high; biseriate rays up to 18 cells high. Ray cells thick-walled, broadly oval to vertically elongate in tangential section, 10–20μ in diameter.

Imperforate tracheary elements: Slightly thick-walled fiber tracheids variously shaped, more or less angled in cross-section, 20–35μ in diameter, non-septate; pits bordered, with slit-like vertical apertures.

Material. A single specimen of mature secondary xylem, measuring 9 × 6 × 5 cm. Structural preservation of the fossil wood is poor.

Holotype. Palaeobotanical Collections, Harvard University, No. 55305.

The affinity of the fossil wood is clearly with the genus *Diospyros*, although it shows a superficial resemblance to the mature secondary xylem of *Carya*. The broad rays of *Carya*, however, are nonstoried, whereas the fossil possesses conspicuously storied, narrow rays.

A survey of all of the available woods of the genus *Diospyros* indicates that the nearest affinity of the fossil is with *D. virginiana* L. Our survey included the study of thin sections of woods of 19 species of the genus and published descriptions of 15 other species (Kanehira, 1921a, pp. 38, 39, *fig. 26*; 1921b, pp. 141–144, *pl. 27, fig. 160*; 1924, pp. 41, 42; Pearson and Brown, 1932, pp. 698, 699, 706–708, *figs. 226, 229*; Reyes, 1938, pp. 408–412, 414–415, *pl. 79, fig. 3, pl. 80, figs. 1–3*; Kribs, 1959, pp. 38, 39, *figs. 129, 358, 359*).

The size and distribution of the vessels of *Diospyros washingtoniana* agree with the distribution pattern in *D. virginiana*. The tangential diameter of the vessels in the fossil wood (40–240μ) is quite close to the measurements secured from comparable secondary xylem of *D. virginiana* (35–220μ). The only obvious difference between the two species is in slightly more thickened vessel walls in *D. virginiana* which also shows vessel groups up to 7 cells. However, both in *D. virginiana* and in the fossil species, the perforations are simple and the intervascular pit-pairs are bordered, alternate, orbicular to oval with linear aperture.

The distribution of parenchyma appears to be almost identical in both as is also the fiber structure.

The xylem rays of the fossil wood and of *Diospyros virginiana* are basically similar, although there are slight differences. In both they are homogeneous to heterogeneous and storied, although the storied structure is slightly irregular in certain areas of the fossil. The rays of *D. virginiana* are 1–3 (mostly 1 or 2) cells broad, often with long, uniseriate wings, whereas in *D. washingtoniana* they are 1 or 2 (mostly 2) cells broad with short uniseriate wings.

Only two other fossil woods of *Diospyros* are known. These are *Diospyros* sp. (Schonfeld, 1925), from the Tertiary of Germany, and *Diospyros* sp. (Slijper, 1932), from the Pliocene of Holland. It is interesting to note that a fossil wood, *Ebenoxylon speciosum*, showing resemblance to *Diospyros* is also known from the Tertiary of California (Platen, 1908).

The genus *Diospyros* is composed of 160 or more species, mostly trees, more abundant in tropical Asia than elsewhere. *Diospyros virginiana* L. is the only representative in temperate North America. It grows in forests, primarily on dry soil, from Rhode Island to southern New York, Iowa, Kansas, Florida, and Texas (Britton, 1908; Munns, 1938, *map 162*).

FAGACEAE

5. **Quercus leuca** Prakash & Barghoorn, sp. nov.   (FIGS. 39–45)

Growth rings: Distinct; wood ring-porous. Transition between early and late wood abrupt.

Vessels: Large vessels in the early wood, 130–390μ in tangential diameter (mean 252μ) (FIGS. 43, 45), solitary, forming a conspicuous band 1–2 pores in width, thin-walled, vessels round to oval in cross-section. Vessel elements up to 400μ long. Perforation plates exclusively simple, usually horizontal. Intervascular pit-pairs alternate, bordered, and round to oval

in shape. Tyloses common. Late-wood vessels small (FIG. 45), $25-75\mu$ in tangential diameter (mean 47μ), scattered in radially aligned, flame-shaped tracts (FIGS. 43, 45) of light-colored tissue, usually solitary, sometimes in pairs, rarely in threes, open, angular in cross-section. Perforation plates and intervascular pit-pairs similar to early-wood vessels.

Parenchyma: Abundant, paratracheal and metatracheal. Paratracheal parenchyma intermingled with the tracheids, (1) forming part of the conjunctive tissue between the early wood vessels and the rays, (2) comprising most of the tissue in the flame-shaped tracts (FIG. 41) in which late-wood vessels are inserted. Metatracheal parenchyma scanty (FIG. 42), restricted to fibrous tracts, mostly in the outer half of the growth ring where it occurs as diffuse, isolated cells or in broken, wavering lines 1 or 2 cells (mostly 1) thick. Parenchyma cells thin walled (FIG. 42), slightly larger than the fiber, very often containing brownish, gummy deposits. Crystalliferous parenchyma abundant, cells slightly swollen (FIG. 39) with rectangular to polygonal crystals.

Xylem rays: Homogeneous (Kribs Homogeneous Type 1), composed of procumbent cells; both narrow and aggregate (FIG. 44); narrow rays mostly uniseriate, rarely partly biseriate, 2–29 cells high; aggregate rays 18–35 cells broad and 14.5 mm. high. Ray cells thin-walled, variously shaped in tangential section and $7-25\mu$ in diameter, sometimes with crystals in swollen elements.

Imperforate tracheary elements: Libriform fibers and vasicentric tracheids. Thick-walled fibers well developed between the spaces among the flame-shaped tracts, polygonal in cross-section, $12-20\mu$ in diameter, nonseptate; pits simple. Vasicentric tracheids intermingled with parenchyma, (1) forming most of the conjunctive tissue between the early-wood vessels and the rays and, (2) comprising part of the flame-shaped tracts in which the late-wood vessels are distributed; pits bordered, round and in 1 or 2 rows, aperture round to elliptic (FIG. 40).

MATERIAL. A single specimen of silicified mature secondary xylem measuring 7.5 $\times$ 2.5 $\times$ 13 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 54916.

The woods of the various species of oaks exhibit considerable variation but possess many features in common. Anatomically, two groups of species can be readily distinguished, the white oak group and the red-black oak group (Record and Hess, 1943, p. 168). These divisions correspond to important botanical differences. The woods can also be grouped into ring-porous, from deciduous trees, and diffuse-porous, from the evergreen or so-called live oaks, but these distinctions are not taxonomic. The red oaks can be distinguished from the white oaks by the following anatomical characters (Brown, Panshin, and Forsaith, 1949, p. 544):

WHITE OAKS	RED OAKS
Transition from early to late wood generally abrupt.	Transition from early to late wood gradual to more or less abrupt.

White Oaks	Red Oaks
Early-wood pores in the heart-wood usually occluded with tyloses.	Early-wood pores in the heart-wood usually open.
Late-wood pores thin-walled, more or less angular, not sharply defined with a hand lens.	Late-wood pores plainly visible with a hand lens, thick-walled, rounded.
Large rays averaging ½–1¼″ in height, frequently taller than 1½″.	Large rays averaging ¼–½″ in height, rarely taller than 1½″.

According to these characters, the fossil wood under consideration belongs to the white oak group. A survey of the available woods of the genus *Quercus* indicates that the nearest affinity of the fossil is with *Quercus alba* L. Our survey included the study of thin-sections of the woods of 86 species of the genus and published descriptions of 15 other species (Sudworth and Mell, 1911, pp. 22–56, *figs. 11–48*; Kanehira, 1921a, pp. 67–71, *pl. 8, figs. 44, 45*; Kanehira, 1924, p. 52; Kanehira, 1940; Pearson and Brown, 1932, pp. 981–996, *figs. 299–304*; Reyes, 1938, pp. 60–62, *pl. 4, figs. 1, 2*; Metcalfe and Chalk, 1950, pp. 1311–1314, *figs. 313G, L*; Greguss, 1947, pp. 41–46, *figs. 18–27*).

The size and distribution pattern of the vessels in early and late wood of *Quercus leuca* and *Q. alba* are almost identical, there being 1 or 2 rows of large vessels in the early wood and small, thin-walled, angular vessels arranged in a flame-like pattern in the late wood. In addition, both in the living and fossil species the perforation plates are exclusively simple and the intervascular pit-pairs are bordered, alternate, and round to oval.

The distribution of parenchyma appears to be almost identical in both, as is the fiber structure. However, a conspicuous difference between the two species is in the crystalliferous parenchyma, which is present in the fossil wood but absent in *Quercus alba.*

The xylem rays of the fossil wood and of *Quercus alba* are basically similar, although there are slight differences in the height of the rays and in the presence of crystals in the ray cells of the fossil. In both they are narrow (mostly uniseriate) and aggregate and composed solely of procumbent cells. However, the rays are 14.5 mm. high and possess large crystalliferous cells in *Q. leuca*, whereas in *Q. alba* they are much higher and do not have crystalliferous cells.

Fossil woods and leaves assigned to *Quercus* are known from the Cretaceous onward from many areas of the earth. Fossil woods have been described under the names *Quercinium* Unger (1842, emend. Brett, 1960), *Quercoxylon* Krausel (1939) and *Quercus* L. These have been listed by Edwards (1931) and Boeshore and Jump (1938). Others not listed and subsequently described are by Ogura (1932), Shimakura (1934), Krausel (1939), Watari (1941, 1952), Hofmann (1944, 1952), Andreanszky (1951), Beyer (1954), Müller-Stöll & Mädel (1957), Boureau (1958), and Brett (1960). All of them differ distinctly from the fossil wood under consideration. Those known from this country are *Quercinium knowltonii* Felix (1896), *Q. lamarense* Knowlton (1899), *Quercus rubida* Beyer

(1954), from the Miocene of Yellowstone National Park; *Quercinium album* Boeshore & Jump (1938), from the Miocene of Idaho; *Quercinium soleroederi* Platen, *Q. wardii* Platen, *Q. anomalum* Platen, *Q. lesquereuxii* Platen, *Q. abromeitii* Platen (Platen, 1908), and *Quercus ricardensis* Webber (1933), from the Miocene and Pliocene, and *Q. agrifolia* Nee (Frost, 1927), from the Pleistocene of California; and *Quercus marcayana* Penhallow (1891), from the post-glacial deposits of Illinois.

Quercus, one of the most important woody genera in the world, is widely distributed in the North Temperate Zone and extends at high altitudes into the tropics as far south as the East Indies in the Old World and the mountains of Colombia and Ecuador in the New World. More than 500 species and varieties of oaks, from low shrubs to stately forest trees, have been described (Record and Hess, 1943).

There are about fifty species of *Quercus* native to the United States. *Quercus alba* L., with which our fossil compares well, grows throughout the entire eastern half of the United States (Munns, 1938, *map 110*). The only oak growing in the state of Washington is *Q. garryana* Douglas (Record and Hess, 1943; Munns, 1938, *map 112*) which also belongs to the white oak group.

HAMAMELIDACEAE

6. **Liquidambar** cf. **styraciflua** L.   (FIGS. 20–24)

Growth rings: Not very conspicuous, delimited by 1 or 2 rows of thick-walled, flattened fibers; wood diffuse-porous (FIG. 20).

Vessels: Small, 30–81μ in tangential diameter (mean 48μ), solitary, in multiples of 2 or 3 (mostly 2), or paired laterally, quite uniform in size and crowded (FIG. 20), thin-walled, oval to slightly angular in cross-section. Vessel elements up to 1070μ long, with tapering, often tailed ends; spiral thickening present, restricted to tapering ends. Perforation plates exclusively scalariform with about 15–30 bars (FIG. 22). Intervascular pit-pairs (FIG. 23) bordered, in transverse rows of 1–3, orbicular to oval or linear through fusion, 7–35μ in diameter. Tyloses absent.

Parenchyma: Scanty, paratracheal and diffuse, either associated with the vessels or found as solitary cells among the fibers; parenchyma cells thin-walled, oval to oblong in cross-section.

Xylem rays: Heterogeneous, nonstoried, 1–3 cells wide; uniseriate rays 5–18 cells high, composed of both upright and procumbent cells; multiseriate rays 2 or 3 (mostly 3) cells broad through the central portion of procumbent cells, with uniseriate extensions above and/or below composed wholly or mainly of upright cells; sometimes with end to end ray fusion; up to 12–20 rays per mm.

Imperforate tracheary elements: Fiber tracheids quadrangular to polygonal in cross-section, 15–35μ in diameter, the walls fairly thick (FIG. 24), non-septate; pits bordered, with vertical or oblique, linear apertures.

MATERIAL. A single specimen of silicified mature secondary xylem

measuring $2 \times 2.5 \times 8$ cm. Structural preservation of the fossil wood poor.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55240.

The fossil wood shows a superficial resemblance to the mature, secondary xylem of *Cercidiphyllum*. However, *Cercidiphyllum* differs from the present fossil wood in having 1- or 2-seriate heterogeneous rays with very frequent end-to-end ray fusion and in having numerous (20–50) bars in the perforation plates.

A survey of all available woods of the *Liquidambar* indicates that the nearest affinity of the fossil is with *Liquidambar styraciflua* L. Our survey included the study of thin-sections of the woods of *L. styraciflua* L., and *L. formosana* Hance.

The size and distribution of the vessels of the fossil wood under consideration agree with the distribution pattern in *Liquidambar styraciflua*. The tangential diameter of the vessels ($30–81\mu$) in the fossil wood is more or less similar to the measurements secured from comparable secondary xylem of *L. styraciflua*. In both, the perforation plates are scalariform, and the intervascular pit-pairs are in transverse rows of 1–3, orbicular to oval or linear through fusion. The distribution of parenchyma appears to be almost identical in both as is the fiber and ray structure. However, a minor difference between the two is in higher and sometimes 4-seriate rays in *L. styraciflua*.

Only three fossil woods showing resemblance to *Liquidambar* are known. These are *Liquidambaroxylon speciosum* Felix (1884), from the Tertiary of Hungary, *L. lecointreae* Houlbert (1910), from the Middle Miocene of Touraine (Edwards, 1931), and *Liquidambar formosana* Hance (Watari, 1952), from the Pliocene of Yokohama City and the Miocene of Honsyu [Honshu], Japan. These species differ from the present fossil. The fossil wood of *Liquidambar formosana* differs in having mostly scalariform intervessel pits, rays 1–4 (mostly 2–3) cells broad with 2 or 3 rays fused frequently, and in possessing a large number of bars (7–39) in the perforation plates.

Liquidambar is represented by about four extant species, three in eastern Asia and one, *Liquidambar styraciflua* L., in America, where it is commonly known as red or sweet gum. This important timber tree is widely distributed throughout the southeastern part of the United States, its northern and western boundaries being from Connecticut, westward through the Ohio Valley to Kansas, and southward through Oklahoma into Texas. It reappears on the mountains of eastern Mexico and the highlands of southern British Honduras and eastern Guatemala and Honduras. It is most abundant and of largest size in wet, rich soil bordering streams or swamps (Record and Hess, 1943; Britton, 1908; Munns, 1938, *map 131*).

JUGLANDACEAE

7. **Carya tertiara** Prakash & Barghoorn, sp. nov.   (FIGS. 14–19)

Growth rings: Distinct, delineated by narrow bands 2 or 3 cells thick,

of flattened, thick-walled fibers; wood semi-ring-porous to diffuse porous. Transition between early and late wood gradual (FIGS. 15, 19).

Vessels: Usually large vessels (FIG. 15) in the early wood, 150–320μ in tangential diameter (mean 214μ), solitary (FIGS. 15, 19) and in radial rows of 2–4 or rarely 5 or 6 cells, thin- to slightly thick-walled, the solitary vessels round to oval in cross-section (FIG. 19). Vessel elements 255–485μ in length with the end walls usually inclined, sometimes truncate, rarely tailed. Perforation plates exclusively simple. Intervascular pit-pairs (FIG. 18) bordered, alternate, orbicular to oval or angular when crowded, 7–12μ in diameter with linear or lenticular apertures. Thin-walled tyloses abundant (FIGS. 15, 17). Late-wood vessels small to medium-sized, 60–150μ in tangential diameter (mean 112.5μ); solitary (FIG. 19) and in radial multiples of 2 or 3 or rarely more; walls thin to conspicuously thickened. Intervascular pit-pairs and perforation plates similar to early wood vessels.

Parenchyma: Paratracheal, metatracheal, metatracheal-diffuse, and terminal. Paratracheal parenchyma varying from isolated cells to uniseriate sheaths partially encircling the vessels. Metatracheal parenchyma (FIGS. 15, 19) in tangential, slightly undulating, usually continuous, sometimes broken, narrow lines 1–3 (usually 1 or 2) cells thick which are arranged irrespective of pores. Diffuse parenchyma scattered among the fibers as groups of two or isolated cells. Terminal parenchyma uniseriate, associated with the flattened fibers at the growth rings. Parenchyma cells thin-walled, oval or tangentially elongate in cross-section, often quite large and crystalliferous (FIGS. 14, 15), 15–40μ in diameter.

Xylem rays: Homogeneous to slightly heterogeneous (FIG. 16), mostly composed of procumbent cells; 1–4 cells wide; uniseriate rays frequent, 2–21 (usually 6–10) cells high; multiseriate rays often fusiform, mostly 3, rarely 4, cells broad and 0.87 mm high with uniseriate wings (up to 11 cells) at one or both ends; broad rays composed either entirely of procumbent cells or rarely with a marginal row of upright cells at one of the ends; up to 9–12 rays per mm. Ray cells 15–30μ in diameter, round to oblong in tangential section, sometimes angular where crowded.

Imperforate tracheary elements: Thick-walled fiber tracheids (FIGS. 15, 19), oval to slightly angular in cross-section, 10–25.5μ in diameter; walls moderately thick with fairly large lumen; non-septate; pits bordered.

MATERIAL. A single specimen of silicified mature secondary xylem measuring approximately 9 × 7 × 3 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55210.

There is close agreement in all structural details with the genus *Carya*, except as noted below. A survey of the available woods of the genus *Carya* indicates that the nearest affinity of the fossil is with *C. leiodermis* Sarg. Our survey included the study of thin sections of the woods of 18 species and published descriptions of two additional species. The latter are *C. tonkiensis* Lecomte (Heimsch and Wetmore, 1939, pp. 655–7, *figs. 21, 22*) and *C. texana* var. *arkansana* (Sarg.) Little (Stark, 1953, p. 31).

The fossil wood of *Carya tertiara* resembles the modern wood of *C. leiodermis* in the distribution pattern of the vessels, in the type of perforation plates, in the nature of the intervascular pit-pairs, in parenchyma distribution, and in the nature of the xylem rays. However, *C. leiodermis* differs from the fossil wood under consideration in having slightly narrower (1–3 cells) and higher (1042μ) xylem rays, in possessing fewer tyloses in the vessels, and in having much less crystalliferous parenchyma which is not swollen like that of the fossil wood. On the other hand, swollen crystalliferous parenchyma is seen in the modern woods of *C. pallida* Engl. & Graebn., *C. cordiformis* K. Koch, *C. aquatica* Nutt., *C. tonkiensis* Lecomte, *C. tomentosa* Nutt., *C. illinoensis* (Wang.) K. Koch, *C. glabra* Sweet, and *C. floridana* Sarg. Since the present fossil wood differs slightly from the modern wood of *Carya leiodermis*, it is assigned to a new species, *C. tertiara* Prakash & Barghoorn.

Only two fossil woods of *Carya* are known. These are *Carya* sp. (Beck, 1942a), from the Upper Miocene of Washington, and *C. protojaponica* (Watari, 1952), from the Miocene of Honsyu [Honshu], Japan. Both these species differ quite distinctly from the present fossil wood. Thus *C. protojaponica* differs from *C. tertiara* in having mostly uniseriate, partly biseriate bands of metatracheal parenchyma and in having homogeneous to decidedly heterogeneous xylem rays 1 or 2, rarely 3 or 4, cells broad. However, in *C. tertiara* the metatracheal parenchyma bands are 1–3-seriate and the xylem rays are 1–4 (mostly 1 and 3) cells broad, homogeneous to weakly heterogeneous.

Similarly, the *Carya* species known from Vantage looks different (Beck, 1942a, *pls. 1731e,b,c,k*) from *C. tertiara*. Unfortunately, a detailed comparison between the two is impossible since Beck's material was not illustrated.

Carya includes about 22 species: one is native to China (*C. cathayensis* Sarg.), a second to Indochina (*C. tonkinensis* Lecomte), a third is restricted to the highlands of Mexico (*C. mexicana* Engelm.), and the remaining nineteen are widely distributed in eastern North America. There are also a number of varieties and hybrids (Stark, 1953). *Carya leiodermis* Sarg. grows in northern Florida, western Alabama, Mississippi, southern Arkansas, Louisiana, and eastern Texas (Little, 1953, p. 87). For a detailed distribution of other species, see Munns (1938), Record and Hess (1943), Fernald (1950), and Little (1953).

LEGUMINOSAE

8. **Albizzia vantagiensis** Prakash & Barghoorn, sp. nov. (FIGS. 51–54)

Growth rings: Distinct; wood diffuse-porous (FIG. 52).

Vessels: Large to medium-sized, sometimes small, 76–245μ in tangential diameter (mean diameter 152μ), encircled by a conspicuous halo of parenchyma (FIG. 52), chiefly solitary, sometimes paired, rarely in rows of 3–4 or even 6 cells, thin-walled, the solitary vessels circular to oval in

cross-section. Vessel elements 178–484μ long, with truncate or slightly tailed ends. Perforation plates exclusively simple. Intervascular pit-pairs (FIG. 51) alternate, sometimes slightly opposite, oval to orbicular, and vestured. Tyloses absent, vessels sometimes plugged with gummy deposits.

Parenchyma: Abundant, paratracheal, paratracheal-zonate, terminal, and metatracheal-diffuse. Paratracheal parenchyma (FIG. 54) forms a narrow or wide halo (up to 5 cells thick) about the vessels or vessel groups, frequently extending laterally beyond proximate rays and usually ending blindly or sometimes uniting with those of other vessels forming paratracheal-zonate parenchyma. Terminal parenchyma sparse, forming a 1- or 2 (mostly 1)-seriate line at the growth ring. Diffuse parenchyma scanty, cells scattered among the fibers. Parenchyma cells 15–30μ in diameter, occasionally crystalliferous.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed chiefly of procumbent cells (FIG. 53), nonstoried, 1–4 cells wide; uniseriate and biseriate rays rare, the uniseriate rays 5–14 cells high; multiseriate rays mostly 3 cells broad and 0.97 mm. high; up to 6–10 rays per mm. Ray cells thin-walled, circular to oval in tangential section, 10–20μ in diameter.

Imperforate tracheary elements: Libriform to semilibriform fibers polygonal in cross-section, 10–20μ in diameter, walls fairly thick (FIG. 54), with a small to fairly large lumen, nonseptate; pits simple.

MATERIAL. Two specimens of silicified secondary xylem. The type specimen measured 5 × 4 × 5 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55237.

The fossil wood most closely resembles the structural features of the leguminous genus *Albizzia*, although it shows a superficial resemblance to the mature secondary xylem of *Artocarpus* (*A. indica*, *A. chaplasha*), particularly as seen in transverse section. The rays in *Artocarpus*, however, are broad and heterogeneous, whereas the fossil possesses homogeneous, narrow rays. A survey of all available woods of the genus *Albizzia* indicates that the nearest affinity of the fossil is with *A. stipulata* Boivin. Our survey included the study of thin-sections of the woods of 14 species of the genus and published descriptions of 8 other species. The latter are *A. montana* Benth., *A. tomentella* Miq. (Moll & Janssonius, 1914, pp. 193–195), *A. lucida* Benth. (Pearson and Brown, 1932, pp. 465–467, *fig. 158*), *A. acle* (Blanco) Merr. (Kanehira, 1924, p. 25; Kribs, 1959, pp. 63, 64, *fig. 163*), *A. gummifera* C. A. Sm., *A. ferruginea* Benth. (Kribs, 1959, pp. 64, 65, *figs. 397–398*), *A. chinensis* (Osb.) Merr. (Reyes, 1938, pp. 117, 118, *pl. 16, fig. 1*) and *A. retusa* Benth. (Schneider, 1916, pp. 116–118, *pl. 2, fig. 15*).

The fossil wood of *Albizzia vantagiensis* resembles the modern wood of *A. stipulata* in the size and distribution pattern of the vessels, in the perforation plates and intervascular pit-pairs, in parenchyma distribution, and the fiber and ray structure. However, *A. stipulata* differs from the fossil in

having partly septate fibers and slightly wider and very low xylem rays. The rays are 1–5 (mostly 2 or 3) cells broad and 0.23 mm. high in *A. stipulata*, whereas they are 1–4 (mostly 3) cells broad and 0.97 mm. high in *A. vantagiensis*.

Albizzia is a rather large genus of small to large trees widely distributed in tropical Asia, Africa, and America. Of the species the best known is probably *A. lebbek* Benth., native to Asia but planted for shade and ornament throughout tropical regions. *Albizzia julibrissin* Boiv., another Asiatic tree, is widely planted for shade and ornament in the southern United States and has become naturalized in woods and thickets from Virginia to Florida and Louisiana (Britton, 1908, p. 519). Its hardy forma *rosea* (Carr.) Rehd. makes favorable growth under climatic conditions as far north as Boston, Massachusetts.

A large number of fossil woods belonging to the family Leguminosae are known. However, woods related to *Albizzia* are limited to two references in the literature. These are *Leguminoxylon albizziae* Krausel (1939), from the Tertiary of Egypt, and *Albizzioxylon sahnii* Ramunjam (1960), from the Cuddalore series (Mio-Pliocene) of the South Arcot district in South India. *Albizzioxylon sahnii* differs from *Albizzia vantagiensis* in its slightly thickened aliform sheaths of parenchyma around the vessels, its septate fibers, and its short xylem rays (5–15 cells high) locally showing a storied tendency. However, in *A. vantagiensis* the fibers are nonseptate and the rays are quite high (5–55 cells) without any storied arrangement.

9. **Gleditsia columbiana** Prakash & Barghoorn, sp. nov.

(Figs. 29, 31–34)

Growth rings: Distinct; wood ring-porous. Transition between the early and late wood quite marked (Figs. 29, 34).

Vessels: Large vessels in the early wood, 100–214μ in tangential diameter (mean diameter 138μ), chiefly solitary (Fig. 34), occasionally paired, forming a band 4–6 vessels in width, thin-walled, the solitary vessels oval to elliptic in cross-section. Vessel elements 130–265μ long. Perforation plates exclusively simple, usually horizontal, sometimes slightly oblique. Intervascular pit-pairs (Fig. 31) vestured, alternate, orbicular to oval or angular (where crowded), 7–10μ in diameter, apertures linear, often coalescent. Vessels frequently plugged with gum deposits. Late-wood vessels small (Figs. 29, 34), barely visible with a hand lens, 15–25μ in tangential diameter (mean 21μ), usually in short radial rows or in small groups embedded in short tangential bands of parenchyma; vessels variously shaped, polygonal, irregular, or occasionally oval. Vessel elements with spiral thickenings (Fig. 32). Perforation plates and intervascular pit-pairs similar to early-wood vessels except slightly smaller.

Parenchyma: Quite abundant (Fig. 34), paratracheal, paratracheal-confluent and terminal. Paratracheal parenchyma (1) composing an appreciable portion of the conjunctive tissue between the vessels and the rays in the early-wood zone, (2) forming fairly extensive tracts about vessels

farther out in the ring, and (3) in the late summer-wood extending from the flanks of the vessels and frequently uniting with parenchyma from proximate vessels and forming short, slightly irregular, 4–10-seriate tangential bands of paratracheal-confluent parenchyma in which the vessels or vessel groups are included (Fig. 29). Terminal parenchyma forming a distinct line passing over into the paratracheal parenchyma of the next ring.

Xylem rays: Homogeneous (Kribs Homogeneous Type II) composed of procumbent cells (Fig. 33), 1–5 cells wide; uniseriate and biseriate rays few, the uniseriate rays usually 6–8 cells high; multiseriate rays fusiform, mostly 3–4 cells broad and 0.86 mm. high; up to 6–8 rays per mm. Ray cells slightly thick-walled, orbicular to oval or sometimes angular in tangential section, $8.5–15\mu$ in diameter.

Imperforate tracheary elements: Libriform fibers oval to angular in cross-section, $10–20\mu$ in diameter, the walls moderately thick, with a fairly large lumen, nonseptate; pits simple.

MATERIAL. A single specimen of silicified mature secondary xylem measuring $7 \times 5 \times 8$ cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55204.

The fossil wood may be assigned to the genus *Gleditsia*, although it also shows resemblance to the mature secondary xylem of *Gymnocladus*. It is rather difficult to distinguish *Gleditsia* from *Gymnocladus* anatomically, but it is proposed to assign the present fossil to *Gleditsia*. However, the possibility remains that it may be the wood of a *Gymnocladus*. Unfortunately, the range of structural variation in the secondary xylem of the fossil is not possible to determine.

Gymnocladus comprises two species, *G. dioicus* (L.) Koch, confined to east-central North America, and *G. chinensis* Baill., known from central China. *Gymnocladus dioicus* differs from the present fossil in having fairly abundant parenchyma forming 1–several(mostly 1)-seriate, occasionally interrupted sheaths about the vessels or vessel groups in the early wood, whereas in the fossil the parenchyma consists of an appreciable portion (usually most) of the conjunctive tissue between the vessels and the rays. Similarly, *G. chinensis* differs from the fossil species in the size and distribution pattern of the vessels in the late-wood zone; in *G. chinensis* they are quite large and usually solitary.

A survey of all available woods of the genus *Gleditsia* indicates that the nearest affinity of the fossil is with *G. triacanthos* L. Our survey included the study of thin-sections of the woods of six species of the genus and published descriptions of two other species. The latter are *G. japonica* Miq. (Kanehira, 1921a, p. 23, *pl. 3, fig. 15*) and *G. formosana* Hay. (Kanehira, 1921b, pp. 93, 94, *pl. 19, fig. 114*).

The size and distribution pattern of the vessels in *Gleditsia columbiana* and *G. triacanthos* (Aw 17464) are almost identical, there being (3)4–6 rows of large vessels (tangential diameter $100–225\mu$ in *G. columbiana*, $125–255\mu$ in *G. triacanthos*) in the early wood and small groups or radial rows

of small vessels (15–25μ in *G. columbiana*, 15–35μ in *G. triacanthos*) embedded in tangential bands of parenchyma in the late wood. In addition, both in *G. triacanthos* and *G. columbiana*, the perforation plates are exclusively simple and the intervascular pit-pairs are alternate, vestured, and orbicular to oval with linear apertures which are often coalescent.

The distribution of parenchyma appears to be almost identical in both, as is the structure of the fibers.

The xylem rays of the fossil wood and of *Gleditsia triacanthos* are basically similar, although there are some differences in the height and breadth of the rays. In both they are homogeneous, composed of procumbent cells of similar size and shape. However, the rays are 1–5 (mostly 3 or 4) cells broad and up to 0.86 mm. high in *G. columbiana*, whereas in *G. triacanthos* they are 1–14 (mostly 6–9) cells broad and the tallest are more than 1.2 mm. high (Brown, Panshin & Forsaith, 1949, *fig. 274*, pp. 576–77). However, in specimen Aw 9454 (Arnold Arboretum wood collections) of *G. triacanthos* examined by us, the rays are only 1–5 (mostly 4 or 5) cells broad but are slightly higher than the present fossil wood.

Only one occurrence of fossil wood of *Gleditsia* (cf. *G. japonica* Miq.), from the Miocene of Japan, is known (Watari, 1952). It differs from the present fossil wood in possessing rays 1–12 cells broad flanked by incomplete sheath cells and in the presence of chambered parenchyma containing solitary crystals.

Gleditsia consists of about eleven species of trees, chiefly Asiatic, usually with the stem and branches heavily armed. It is represented in the Western Hemisphere by only three species, two in eastern North America, the third in southern South America (Record and Hess, 1943). *Gleditsia triacanthos* L. is a large forest tree of scattered occurrence throughout most of the eastern half of the United States, achieving optimum development along small streams in southern Indiana and Illinois (Munns, 1938, *map 142*). *Gleditsia aquatica* Marsh. is a smaller tree of river-swamps, from Florida to Texas, northward to North Carolina, southern Indiana and Illinois, and southeastern Missouri. The single species of the Southern Hemisphere, *G. amorphoides* (Griseb.) Taub., grows in northern Argentina, Bolivia, and southern Brazil.

PLATANACEAE

10. **Platanus americana** Prakash & Barghoorn, sp. nov. (FIGS. 8–13)

Growth rings: Distinct (FIG. 10), marked by a few rows of tangentially flattened fibers.

Vessels: Small (FIG. 10), 30–77μ in tangential diameter (mean diameter 54μ), somewhat smaller in the late summer wood. Vessels solitary and in irregular groups of 2–5 cells, numerous and crowded, and more or less evenly distributed through most of the annual ring (FIG. 10), about 140 per sq. mm. in the early wood, somewhat less abundant and widely spaced in the late summer wood; vessels variously shaped in cross-section (FIG.

10), oval, elliptical, nearly round with sides in contact much flattened, and angular where crowded, those first formed usually compressed tangentially. Vessel elements 305–765μ in length usually with oblique often tailed ends. Perforation plates both simple and scalariform (FIGS 12, 13); simple perforation large, oval to elliptic in shape and more numerous than the scalariform; scalariform perforations uncommon, bars 2–11 in number, fine, widely spaced and occasionally bifurcate (FIG. 12). Intervascular pit-pairs bordered (FIG. 8), opposite to subopposite on the vessel wall, often loosely arranged, oval to orbicular or elongated in shape, 9–12μ in diameter, with slit-like apertures. Tyloses absent. Vessel distribution graded porous (FIG. 10).

Parenchyma: Scanty, paratracheal and metatracheal-diffuse; paratracheal parenchyma restricted to occasional cells never forming a sheath around the vessels; diffuse parenchyma sporadically distributed as isolated cells among the fibers; parenchyma cells oval to elliptic in cross-section.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed of procumbent cells (FIG. 11), 2–15 cells wide; multiseriate rays fusiform (FIG. 11), mostly 6–15 cells broad and 3.84 mm. in height with pointed or blunt ends, often arranged closely and vertically upon each other so as to appear as parts of the same ray dissected into smaller units; up to 3–4 rays per mm. Ray cells thin-walled, oval to oblong (sometimes polygonal) in tangential section.

Imperforate tracheary elements: Thick-walled fiber tracheids with a small lumen, polygonal in cross-section (FIG. 9), 15–25μ in diameter; nonseptate, about 1020μ in length; pits bordered with vertical slit-like aperture.

MATERIAL. A single specimen of silicified mature secondary xylem broken into a number of fragments.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55218.

This fossil wood shows a superficial resemblance to the mature secondary xylem of *Euptelea* and *Fagus*, particularly as seen in transverse section. However, the broad rays of *Euptelea* are conspicuously heterogeneous, whereas the fossil possesses homogeneous multiseriate rays. Similarly, *Fagus* differs from the present fossil wood in having oak-type rays, i.e., large, broad rays accompanied with numerous, small, uniseriate rays. A survey of all available woods of the genus *Platanus* indicates that the nearest affinity of the fossil within this genus is with *P. wrightii* S. Wats. Our survey included the study of thin sections of the woods of *P. wrightii*, *P. occidentalis* L. and *P. racemosa* Nutt., and published descriptions of three others. The latter are *P. orientalis* L. (Metcalfe and Chalk, 1950, p. 1281, *figs. 300a,b*; Greguss, 1947, pp. 74, 75, *fig. 68*), *P. acerifolia* Willd. (Henderson, 1953, p. 6, *fig. 308*) and *Platanus* sp. (Dadswell and Record, 1936, p. 23, *pl. 2, fig. 3*). The secondary xylem of *P. wrightii* is characterized by small, solitary or irregular groups of 2–5 vessels. There is a conspicuous difference in diameter between the vessels of the early wood and those of the late wood (Brush, 1917, pp. 493, 494, *pl. 33*). The

size and distribution of the vessels in *P. americana* agree with the distribution pattern in the modern *P. wrightii*. Mean tangential diameter of vessels in *P. americana* (54μ) is quite comparable to the measurements secured from comparable secondary xylem of *P. wrightii* (61μ). In both *P. wrightii* and the fossil species the intervascular pit-pairs are bordered, oval to elongate, usually opposite, sometimes alternate, and often loosely arranged in vertical rows. Similarly, simple as well as scalariform perforations are present in both *P. wrightii* and the fossil species. However, in *P. wrightii* the scalariform perforations are more numerous than the simple type and are characterized by 1–20 (most frequently 6–15) closely spaced, fine bars which are sometimes bifurcate. Contrary to this, in *P. americana* simple perforations are more numerous than the scalariform type which are characterized by 2–11 widely spaced bars. It is evident that in this respect the fossil species is more highly specialized than the living species *P. wrightii*. However, in *P. occidentalis*, the perforation plates are simple, for the most part, or occasionally scalariform with a few bars (Brown, Panshin & Forsaith, 1949, p. 570), a condition quite comparable to the fossil wood under consideration.

Very little wood parenchyma is present in the fossil *Platanus* and sometimes it becomes quite difficult, in cross-section, to distinguish parenchyma from the tracheary elements because of the absence of the secondary walls of the latter, which thus resemble parenchyma cells. However, in longitudinal sections it is possible to distinguish between them. The distribution of parenchyma appears to be similar in both, as is the fiber structure; but a conspicuous difference is in the quantity of diffuse parenchyma which is quite abundant in *Platanus wrightii* but much less so in the fossil wood. In *P. wrightii*, parenchyma occurs both as isolated cells and as uniseriate lines of 2–4 or rarely more cells, whereas in *P. americana* it occurs only as diffuse solitary cells.

The xylem rays of the fossil wood and of *Platanus wrightii* are basically similar, although there are slight differences in frequency of broad, multiseriate rays. In both they are very high, usually broad, and homogeneous, composed of round to oval procumbent cells. However, the rays are 2–15 (mostly 6–15) cells broad in *P. americana*, whereas in *P. wrightii* they are 1–14 (rarely uniseriate, mostly 10–14) cells broad.

A number of fossil woods belonging to the family Platanaceae are known from various localities in the world. The woods have been included under the names *Plataninium* Unger (emend. Vater, 1884), *Platanoxylon*, and *Platanus* (Windisch, 1886; Kaiser, 1890; Felix, 1894; Platen, 1908; Schonfeld, 1930; Slijper, 1932; Stockmans, 1936; Hofmann, 1952; Andreánszky, 1951; Beyer, 1954). Those known from this country are *Plataninium crystallophilum* Platen (1908), from the Tertiary of Arizona, *P. pacifica* Platen (1908), from the Miocene of California (Nevada County), *P. knowltonii* Platen (1908), and *Platanus haydenii* (Felix) Beyer (1954), the last two from the Miocene of Amethyst Mountain in the Yellowstone National Park. The general agreement between these and the Vantage fossil wood is close.

The only two fossil woods described under *Platanus* are *Platanus* sp. (Slijper, 1932) and *Platanus haydenii* (Beyer, 1954). Slijper's *Platanus,* from the Pliocene of Reuver, Limburg, Holland, differs from *P. americana* in having spiral thickenings in the vessels and xylem rays 8–10 cells wide (Slijper, 1932, pp. 27, 28, *fig. 3*). Spiral thickenings are not found in the vessels of *P. americana* and the rays are 2–15 (mostly 6–15) cells broad. Similarly, *P. haydenii* (Felix) Beyer, (1954) also differs from *P. americana* in having exclusively simple perforation plates and narrower (3–10-seriate) rays. However, in *P. americana* both simple and scalariform perforation plates are present and the rays are mostly 6–15 cells broad.

Platanus, the only genus of the Platanaceae, includes about eleven species of large trees, three in southern Europe and Asia, eight in temperate North America (Record and Hess, 1943). The largest and the best known species in the United States is *P. occidentalis* L., which is common along streams and lakes and throughout most of the eastern half of North America, growing at optimum in the lower Ohio and Mississippi Valleys (Record and Hess, 1943; Britton, 1908). *Platanus wrightii* S. Wats. and *P. racemosa* Nutt. occur in the southwestern United States and northern Mexico (Record and Hess, 1943; Munns, 1938, *map 132*). Five other species are found only in Mexico.

ULMACEAE

11. Ulmus miocenica Prakash & Barghoorn, sp. nov.   (Figs. 1–7)

Growth rings:. Very distinct; wood ring-porous. Transition between early and late wood quite marked (Figs. 1, 4).

Vessels: Large vessels in the early wood, 81–179μ in tangential diameter (mean 118μ), chiefly solitary, usually arranged in one, sometimes in two rows (Fig. 1), occasionally associated with or interspersed by clusters or radial rows of small vessels (Fig. 4), thick-walled, the solitary vessels circular to oval in cross-section. Vessel elements 153–367μ long. Perforation plates exclusively simple, usually horizontal, sometimes slightly oblique. Intervascular pit-pairs (Fig. 5) bordered, alternate to subopposite on the vessel wall, orbicular or angular where crowded, 8–10μ in diameter with circular or elongate aperture, occasionally confluent. Late-wood vessels small (Figs. 1, 4), 30–70μ in tangential diameter (mean 51μ), grouped in more or less continuous wing-like or festoon-like tangential or oblique bands, usually polygonal due to clustering, occasionally round to oval in form. Vessel elements 112–163μ in length, with spiral thickenings (Fig. 6). Perforation plates and intervascular pit-pairs similar to early wood vessels except slightly smaller. Thin-walled tyloses quite common.

Parenchyma: Paratracheal and metatracheal-diffuse. Paratracheal parenchyma (Fig. 4) quite abundant, contiguous to (but never forming a continuous sheath around) the large vessels of the early wood, marginal to and included in the clusters of smaller early-wood vessels and vascular tracheids (Fig. 4), and marginal to and included in the clusters of wavy bands of late-wood vessels and vascular tracheids. Diffuse parenchyma

sparse, scattered among the fibers, often in contact with the rays. Chambered parenchyma quite abundant (FIG. 7) usually consisting of eight or more elements per strand bearing crystals in a vertical series. Crystalliferous parenchyma usually associated with the xylem rays. (FIG. 3, 7).

Xylem rays: Homogeneous (Kribs Homogeneous Type 1) composed of procumbent cells (FIGS. 3, 7), 1–4 cells wide; uniseriate rays rather scanty, 2–10(14) cells high; multiseriate rays fusiform, mostly 3 or 4 cells broad and 0.76 mm. high; up to 6–10 rays per mm. Ray cells (FIG. 7) slightly thick-walled, circular to oval in tangential section and 10–15μ in diameter.

Imperforate tracheary elements: Libriform fibers and vascular tracheids. Libriform fibers circular to polygonal with rounded corners (FIG. 4) in cross-section. 10–15μ in diameter, the walls fairly thick, with a small lumen, nonseptate; interfiber pits simple. Vascular tracheids present both in the early-wood porous zone and in the wavy bands of late-wood vessels.

MATERIAL. A single specimen of silicified mature secondary xylem measuring 6 × 4 × 4 cm.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55213.

Structural features of the fossil wood indicate, after extensive comparison, that its closest affinities are with the modern genus *Ulmus*. There is close agreement in all structural details except as noted below. A survey of all available woods of the genus *Ulmus* indicates that the nearest affinity of the fossil is with *U. americana* L. Our survey included the study of thin sections of the woods of 14 species of the genus supplemented by published descriptions of five other species. The latter are *U. sieboldii* Daveau (Kanehira, 1921a, p. 55, *pl. 6, figs. 34, 35*), *U. uyematsui* Hay. and *U. parvifolia* Jacq. (?) (Kanehira. 1921b, p. 211, *pl. 40, fig. 237*), *U. Wallichiana* Planch., and *U. lancifolia* Roxb. (Pearson and Brown, 1932, pp. 897–902, *figs. 279, 280*).

The size and distribution pattern of the vessels in the early wood of *Ulmus miocenica* and *U. americana* are almost identical, there being one or two rows of large vessels. However, the pattern of vessel arrangement in the late wood differs slightly in the fossil species. In *U. americana* there are usually almost parallel patches of small vessels separated from each other, whereas these patches are larger, closer, and slightly oblique in the fossil wood. Both in *U. americana* and in the fossil species the perforations are simple and the intervascular pit-pairs are bordered, usually alternate, orbicular or angular through crowding, and with circular to extended apertures.

The distribution of parenchyma appears to be almost identical in both, as is the fiber structure. However, a conspicuous difference between the two species is in the quantity of crystalliferous parenchyma which is quite frequent in the fossil wood but much less so in *Ulmus americana*.

The xylem rays of the fossil wood and of *Ulmus americana* are basically similar although there are slight differences in the height and breadth of the rays. In both they are closely spaced and homogeneous, composed of

procumbent cells of similar size and shape. However, the rays are 1–4 cells broad and up to 40 cells high in *U. miocenica*, whereas in *U. americana* they are up to 7 (mostly 4–6) cells broad and lower (up to 28 cells high: Brown, Panshin & Forsaith, 1949).

Determination of the degree of affinity to modern species of the genus leads to only a few observable differences between the Upper Miocene wood and that of the modern *Ulmus americana*. These differences are mainly limited to the distribution pattern of the late-wood vessels and the height and breadth of the xylem rays.

Sixteen species of fossil woods assigned to the family Ulmaceae have been reported hitherto. These have been described under the names *Ulminium* Unger (1842), *Ulmoxylon* Kaiser (1879), *Ulmus* L., *Zelkova* Spach, *Celtis* L., and *Celtoxylon*. Of these sixteen, five are recorded as species of extant genera, two each of *Zelkova* and *Ulmus*, viz., *Z. wakimizui* (Watari) Watari (1952), *Z. zelkoviformis* (Watari) Watari (1952), *Ulmus* sp. (Fietz, 1926a,b), *U. crystallophora* Watari (1952), and one of *Celtis* (Shimakura, 1936). The remaining eleven are designated as species of *Ulminium*, *Ulmoxylon*, and *Celtoxylon* (Pampaloni, 1904; Penhallow, 1907; Platen, 1908; Nagelhard, 1922; Greguss, 1943; Hofmann, 1944; Boureau, 1957).

Our fossil wood under consideration differs from all the species of *Ulminium* and *Ulmoxylon* and from both the fossil species of *Ulmus* recorded. Thus *Ulmus crystallophora* Watari, from the Miocene of Honsyu [Honshu], Japan, differs from *U. miocenica* in having 2–4-seriate large vessels in the early wood and in possessing rays 1–6 cells wide and up to 1020μ in height. However, in *U. miocenica* the large early-wood vessels are mostly in one row and the xylem rays are only 1–4 cells wide and up to 620μ in height.

It is interesting to note that a fossil wood, *Ulmoxylon simrothii*, showing resemblance to modern elms is also known from the Pliocene of California (Platen, 1908, pp. 26, 27, *pl. 1, figs. 5, 6*). This fossil wood differs from *Ulmus miocenica* in a number of features, especially in having small, radially elongated vessels (97.5μ in tangential diameter) mostly isolated in the early wood and forming a ring-like zone and in having numerous xylem rays five or six cells broad which are often weakly heterogeneous.

Ulmus, with about twenty species of small to very large trees, is widely distributed throughout the North Temperate Zone, except in the western half of North America. Of the six species native to the United States, three are of commercial importance. *Ulmus rubra* Mühl. (*U. fulva* Michx.) is of scattered occurrence over the entire eastern half of the country and southeastern Canada. *Ulmus thomasii* Sarg. occurs in western Vermont to extreme southern Quebec, New York, Ohio, Indiana, Kentucky, Illinois, Iowa, Missouri, and parts of adjoining states, being at its best in the Ohio Valley. *Ulmus alata* Michx. grows in the south-central states. *Ulmus americana* L. has a natural range including the eastern half of the United States, extending from the Great Plains to the Atlantic and from Canada to the Gulf of Mexico (Munns, 1938, *map 120*; Record and Hess, 1943).

Ulmus serotina Sarg. is known to inhabit banks and bluffs from southern Illinois and southern Kentucky to Arkansas, Georgia, and Alabama, and is thus one of the most restricted in geographic distribution. *Ulmus crassifolia* Nutt. prefers moist soil and is most abundant in river valleys from southwestern Tennessee, Arkansas to Mississippi, Louisiana, southern Oklahoma, Texas, and northern Mexico (Britton, 1908). The only species in tropical America is mexican elm, *U. mexicana* (Liebm.) Planch. growing in lower mountain regions from Veracruz and Oaxaca, Mexico, southward to Panama and northwestern Colombia (Record, 1924).

12. **Ulmus pacifica** Prakash & Barghoorn, sp. nov.   (FIGS. 35–38)

Growth rings: Distinct (FIG. 37); wood semi-ring porous. Transition between early and late wood not very marked.

Vessels: Large vessels (FIG. 37) in the early wood, 70–160μ in tangential diameter (mean 114μ), chiefly solitary, arranged in one row, very rarely associated with small vessels, thin-walled, the solitary vessels usually circular to oval in cross-section. Perforation plates exclusively simple, horizontal to slightly oblique. Intervascular pit-pairs bordered, alternate to subopposite on the vessel wall (FIG. 36) oval to orbicular, 5–8μ in diameter and often somewhat loosely arranged, the aperture circular. Late-wood vessels (FIG. 37) slightly smaller, 40–120μ in tangential diameter (mean 76.5μ), almost always clustered in irregular groups, often forming radial rows, very rarely in wing- or festoon-like oblique bands, usually round to oval, sometimes variously shaped due to clustering. Vessel elements with spiral thickenings. Perforation plates and intervascular pit-pairs similar to early-wood vessels. Thin-walled tyloses quite common.

Parenchyma: Paratracheal and metatracheal-diffuse. Paratracheal parenchyma not abundant, occurring in association with the large early-wood vessels but never forming a continuous sheath, marginal to and sometimes included in the groups of late-wood vessels and vascular tracheids. Diffuse parenchyma very scanty, occurring as scattered cells among the fibers.

Xylem rays: Homogeneous (Kribs Homogeneous Type 2), composed of procumbent cells (FIG. 38), 1–8 cells wide, uniseriate and biseriate rays rare; uniseriate rays 2–9 cells high; multiseriate rays fusiform (FIG. 38), mostly 5–7 cells broad and 1.07 mm. high; up to 6–10 rays per mm. Ray cells thin-walled, circular to oval, sometimes vertically elongate in tangential section and 7–12μ in diameter.

Imperforate tracheary elements: Libriform fibers and vascular tracheids. Libriform fibers round to polygonal in cross-section (FIG. 35), 10–15μ in diameter, thick-walled, with a small lumen, non-septate; pits simple. Vascular tracheids often associated with the groups of late-wood vessels.

MATERIAL. A single specimen of silicified mature secondary xylem measuring 11 × 8 × 4 cm. Structural preservation of the fossil is poor.

HOLOTYPE. Palaeobotanical Collections, Harvard University, No. 55229.

There is close agreement with *Ulmus* in all structural details except as noted below. The fossil wood shows a superficial resemblance to the mature secondary xylem of *Ptelea*. However, the xylem rays of *Ptelea* are heterogeneous and the vessels are devoid of tyloses, whereas the fossil possesses homogeneous rays and the vessels are tylosed.

The fossil wood does not compare in all details with any extant species of *Ulmus*, but it shows some structural resemblance with *Ulmus mexicana* (Liebm.) Planch. Although both in the fossil and *Ulmus mexicana* the vessel distribution is semi-ring-porous and there is little difference in vessel size in the early- and late-wood zones, the frequency of the vessels in the fossil wood is greater than in *U. mexicana* in which the vessel groups or rows are smaller and more widely separated than the fossil under consideration. However, the vessel perforations and intervascular pit-pairs are similar in both.

The distribution and amount of parenchyma is different in the fossil and extant *Ulmus mexicana*. The paratracheal parenchyma is more abundant in *U. mexicana* than in *U. pacifica* and the metatracheal parenchyma often forms broken tangential bands one to three cells wide in *U. mexicana*. Such parenchyma bands are not known in the fossil under consideration. Furthermore, in *U. mexicana* there are usually several layers of parenchyma cells associated with the growth rings, a type of parenchyma not found in *U. pacifica*; and crystalliferous parenchyma is quite common in *U. mexicana* but lacking in the fossil wood.

The xylem rays of the fossil wood and of *Ulmus mexicana* are basically similar, although there are some differences in height and breadth. In both they are closely spaced and homogeneous, composed of procumbent cells. However, the rays are 1–8 cells broad and 1.07 mm. high in *U. pacifica*, whereas in *U. mexicana* they are only 1–6 cells broad and lower, including uniseriate and biseriate rays quite frequently. Uniseriate and biseriate rays are very rare in the present fossil wood.

Lastly, the fiber structure appears to be almost identical in both. The fibers are nonseptate, thick walled, and usually polygonal in cross-section, with simple pits.

The general agreement in, as well as the numerous microscopic details of, anatomical structure provides sufficient evidence to identify the Vantage fossil wood as *Ulmus*. However, there are no extant species of *Ulmus* with which the fossil wood can be compared very closely. Therefore, it is quite possible that the fossil wood belongs to an extinct species somewhat differing from modern *Ulmus* species but exhibiting the general anatomical organization of the genus.

DISCUSSION

The present study of the petrified woods from the Columbia Basalts at Vantage has given valuable information regarding the changes in the forest vegetation of the western United States since Miocene times. In the present paper, the authors describe fossil woods of *Acer, Diospyros,*

Quercus, Liquidambar, Carya, Albizzia, Gleditsia, Platanus, and *Ulmus*. A study of the present-day distribution of these genera reveals important clues to the migration of these forms since the Upper Miocene. At present, the genera *Diospyros, Liquidambar, Carya, Gleditsia*, and *Ulmus* are largely limited to the eastern United States. On the other hand, the genus *Platanus* grows in both the eastern and the southwestern United States, while *Acer* and *Quercus* occur almost throughout. The genus *Acer* attains its greatest development in eastern Asia and the eastern United States and only a few species are now found in the western part of the country. Among the species of *Quercus*, *Q. alba* L., with which the fossil wood of *Q. leuca* Prakash & Barghoorn compares well, grows throughout the entire eastern half of the United States. *Albizzia*, at present, is widely distributed in tropical Asia, Africa, and America. However, *A. julibrissin* Boiv., an Asiatic tree, long planted for ornament and shade in the southern United States, has become naturalized from Virginia to Florida and Louisiana. From this, it is evident that the Vantage forest is composed of the eastern, the western, and the exotic elements, particularly those of Asia. It, therefore, seems quite likely that during the Miocene the present forest vegetation of this country was more widely distributed than at the present time. It appears to have become restricted after the Miocene as a result of climatic and orographic change. The complete extinction of the deciduous forest at Vantage and neighboring areas seems to have been accelerated with the late Tertiary rise of the Cascade Mountains and their concomitant effect on depleting the moisture from the Pacific air masses. The effect of increasing cold resulting from the oncoming Pleistocene and the failure of remigration in post-glacial times also helped to accelerate this process. A further study of this flora, which will throw more light on the past vegetation of the northwest United States, its trend of migration, and a number of other related problems, is in progress.

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EXPLANATION OF PLATES

PLATE 1

FIGS. 1–7. Wood of *Ulmus miocenica*: 1, transverse section, × 26 — note the ulmiform bands of late-wood vessels; 2, tangential section, × 75; 3, tangential section showing shape, size, and distribution of xylem rays, × 26 — also note chambered parenchyma associated with rays; 4, transverse sections showing the cellular structure of various tissues, × 100; 5, intervascular pitting, × 320; 6, spiral thickening of late-wood vessels, × 130; 7, tangential section showing a xylem ray and chambered parenchyma, × 100. FIGS. 8–9. Wood of *Platanus americana*: 8, intervascular pitting, × 320; 9, transverse section showing the details of the structure, × 75.

PLATE 2

FIGS. 10–13. Wood of *Platanus americana*: 10, transverse section, × 26 — note vessel distribution and growth rings forming a notch where they meet the rays; 11, tangential section showing shape and size of xylem rays, × 26; 12, scalariform perforation plate, × 90; 13, simple perforation plate, × 90. FIGS. 14–18. Wood of *Carya tertiara*: 14, swollen chambered parenchyma with crystals, × 110; 15, transverse section, × 40 — note the distribution of metatracheal parenchyma cells often with crystals; 16, tangential section showing form and distribution of the rays, × 35; 17, tyloses in the vessels, × 90; 18, intervascular pitting, × 90.

PLATE 3

FIG. 19. Wood of *Carya tertiara*: 19, transverse section, × 26 — note the vessel and parenchyma distribution. FIGS. 20–24. Fossil wood of *Liquidambar styraciflua*: 20, transverse section, × 26 — note vessel distribution; 21, tangential section, × 90; 22, scalariform perforation plate, × 150; 23, intervascular pitting, × 230; 24, transverse section, × 150. FIGS. 25–27. Wood of *Acer puratanum*: 25, transverse section, × 90; 26, spiral thickenings, × 90; 27, transverse section, × 26 — note vessel distribution.

PLATE 4

FIG. 28. Wood of *Acer puratanum*: 28, tangential section showing shape and size of the xylem rays, × 90. FIG. 29. Wood of *Gleditsia columbiana*: 29, transverse section, × 65 — note vessel distribution in the late wood. FIG. 30. Wood of *Acer puratanum*: 30, intervascular pitting, × 190. FIGS. 31–34. Wood of *Gledtsia columbiana*: 31, intervascular pitting, × 280; 32, spiral thickening, × 310; 33, tangential section, × 65 — note ray distribution; 34, transverse section, × 26 — note vessel distribution in early and late wood. FIGS. 35–36. Wood of *Ulmus pacifica*: 35, transverse section, × 125; 36, intervascular pitting, × 220.

PLATE 5

FIGS. 37, 38. Wood of *Ulmus pacifica*: 37, transverse section, × 40 — note vessel distribution; 38, tangential section, × 50 — note xylem rays, tyloses in vessels. FIGS. 39–43. Wood of *Quercus leuca*: 39, transverse section showing parenchyma and fiber cells, × 140 — note slightly enlarged cells of parenchyma often with crystals; 40, tracheid pitting, × 310; 41, transverse section showing late-wood vessels, × 65 — note thin-walled, angular pores; 42, transverse section showing the distribution of metatracheal parenchyma, × 65; 43, transverse section, × 26 — note large vessels in early wood and smaller vessels in late wood arranged in flame-shaped tracts.

PLATE 6

FIGS. 44, 45. Wood of *Quercus leuca*: 44, tangential section, × 75 — note part of an aggregate ray and numerous uniseriate rays; 45, another transverse section showing three growth-zones, × 18 — note the distribution of vessels in early and late wood. FIGS. 46–50. Wood of *Diospyros washingtoniana*: 46, part of tangential section showing the ray structure, × 105; 47, transverse section showing vessel distribution, × 35; 48, tangential section, × 40 — note the storied arrangement of the xylem rays; 49, part of transverse section highly magnified. × 70 — note thick vessel wall; 50, tyloses, × 90. FIG. 51. Wood of *Albizzia vantagiensis*: 51, intervascular pitting, × 280.

PLATE 7

FIGS. 52–54. Wood of *Albizzia vantagiensis*: 52, transverse section, × 26 — note vessel and parenchyma distribution forming eyelets around vessels; 53, tangential section, × 65 — note shape, size, and distribution of xylem rays; 54, transverse section magnified to show parenchyma distribution, × 65. FIGS. 55–57. Wood of *Acer beckianum*: 55, transverse section, × 50 — note vessel distribution and broad xylem rays; 56, part of Fig. 55 magnified to show structural details, × 80; 57, intervascular pitting, × 220.
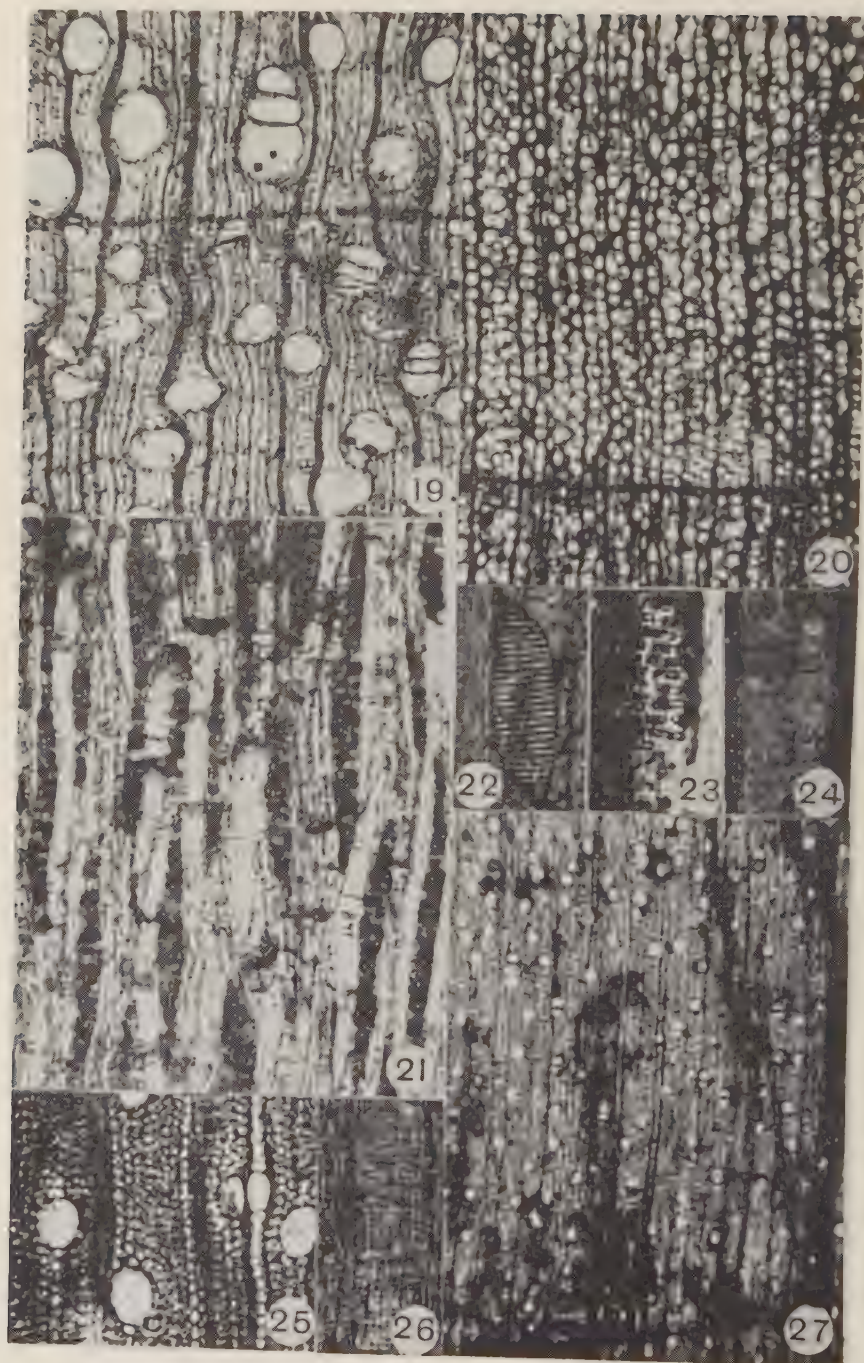
PLATE 8

FIG. 58. Wood of *Acer beckianum*: 58, tangential section, × 65. FIGS. 59–63. Wood of *Acer olearyi*: 59, simple perforation and spiral thickening, × 225; 60, intervascular pitting, × 225; 61, transverse section, × 105; 62, transverse section, × 38 — note solitary vessels and narrow rays; 63, tangential section showing xylem rays, × 105.
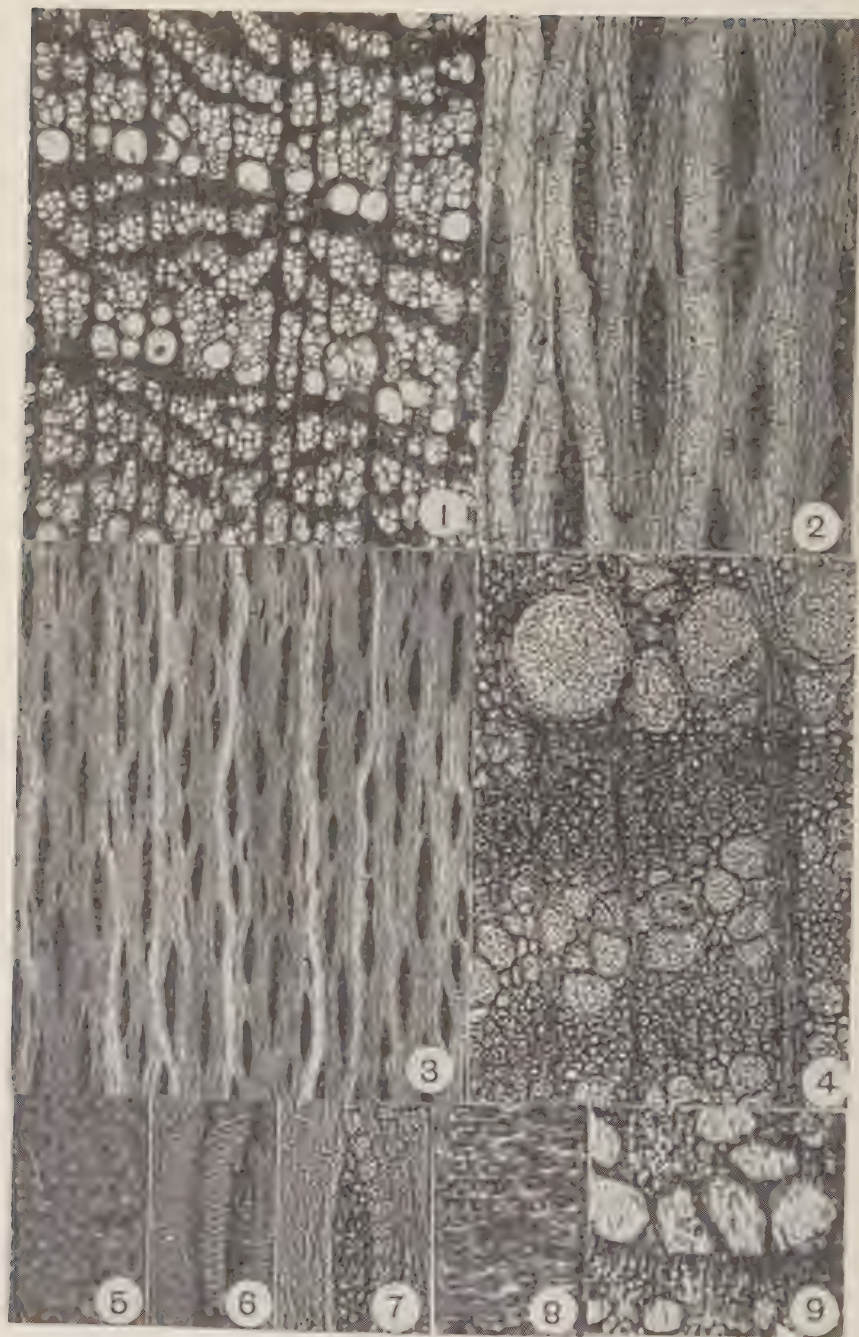
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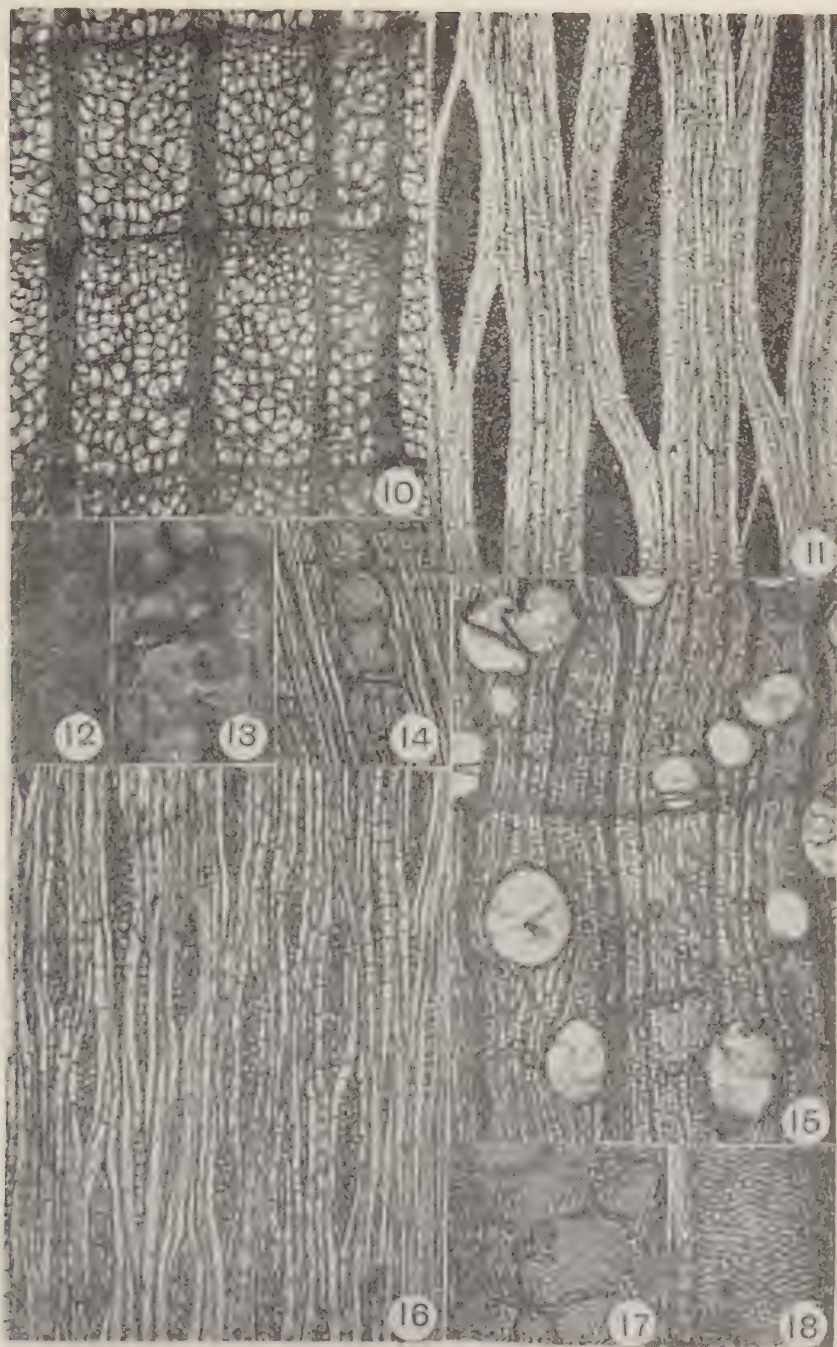
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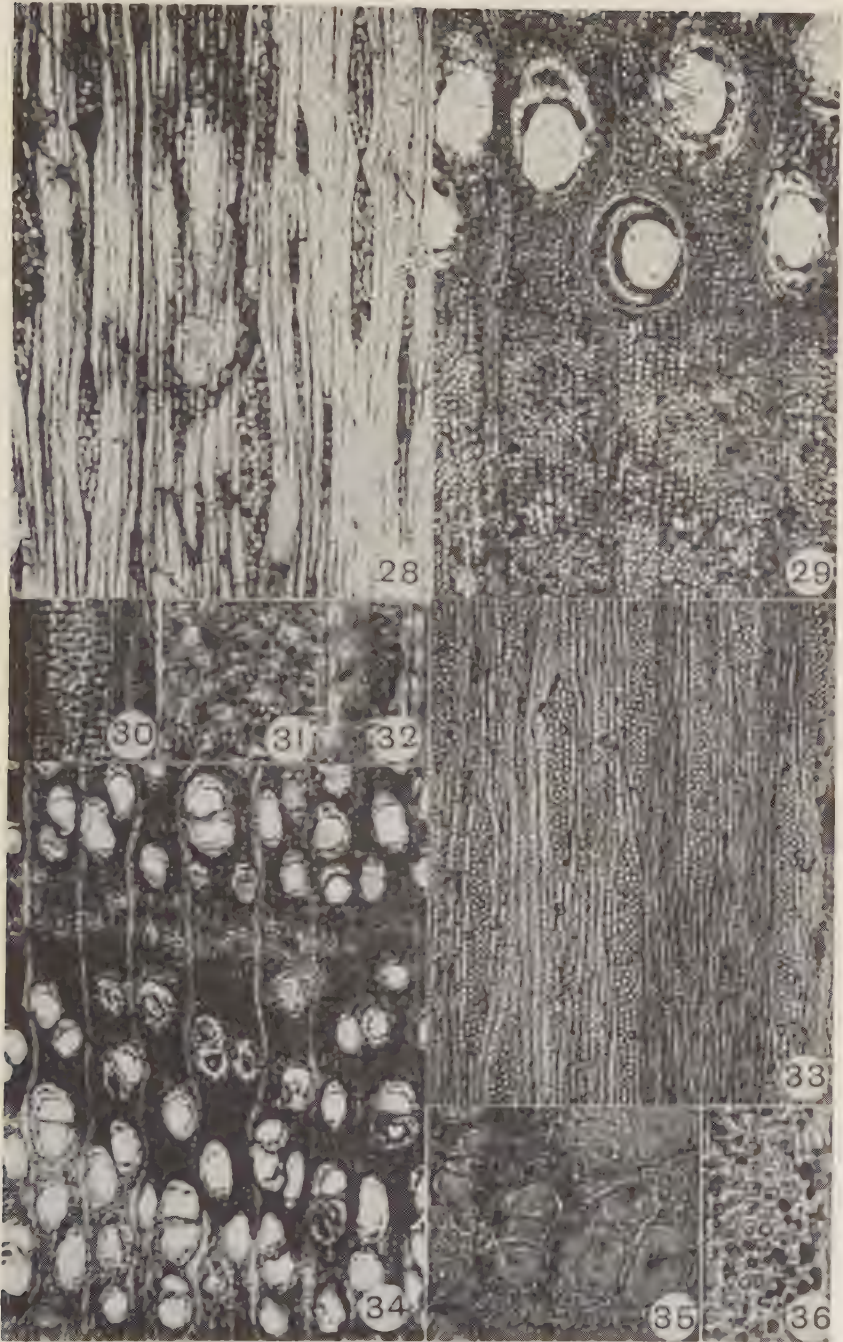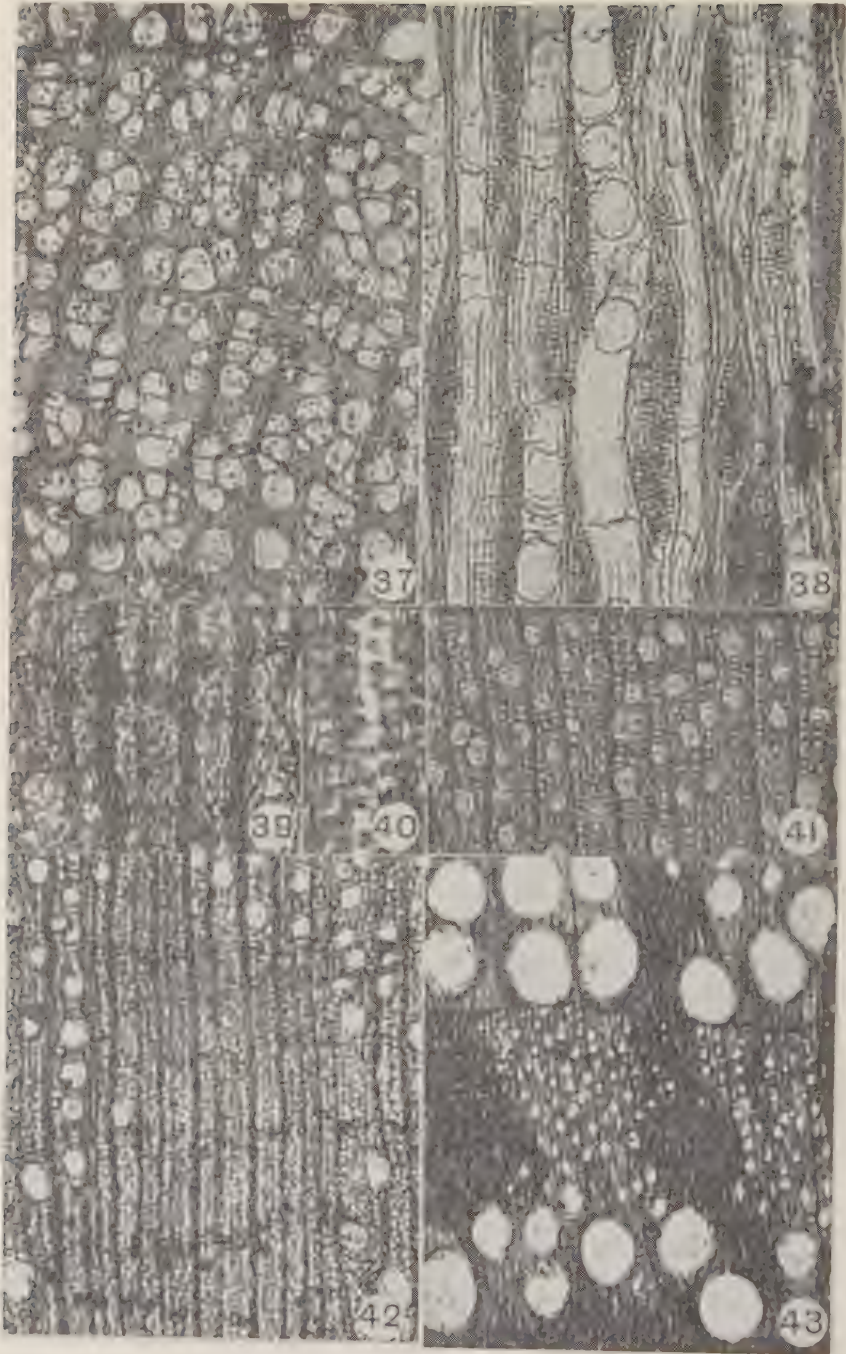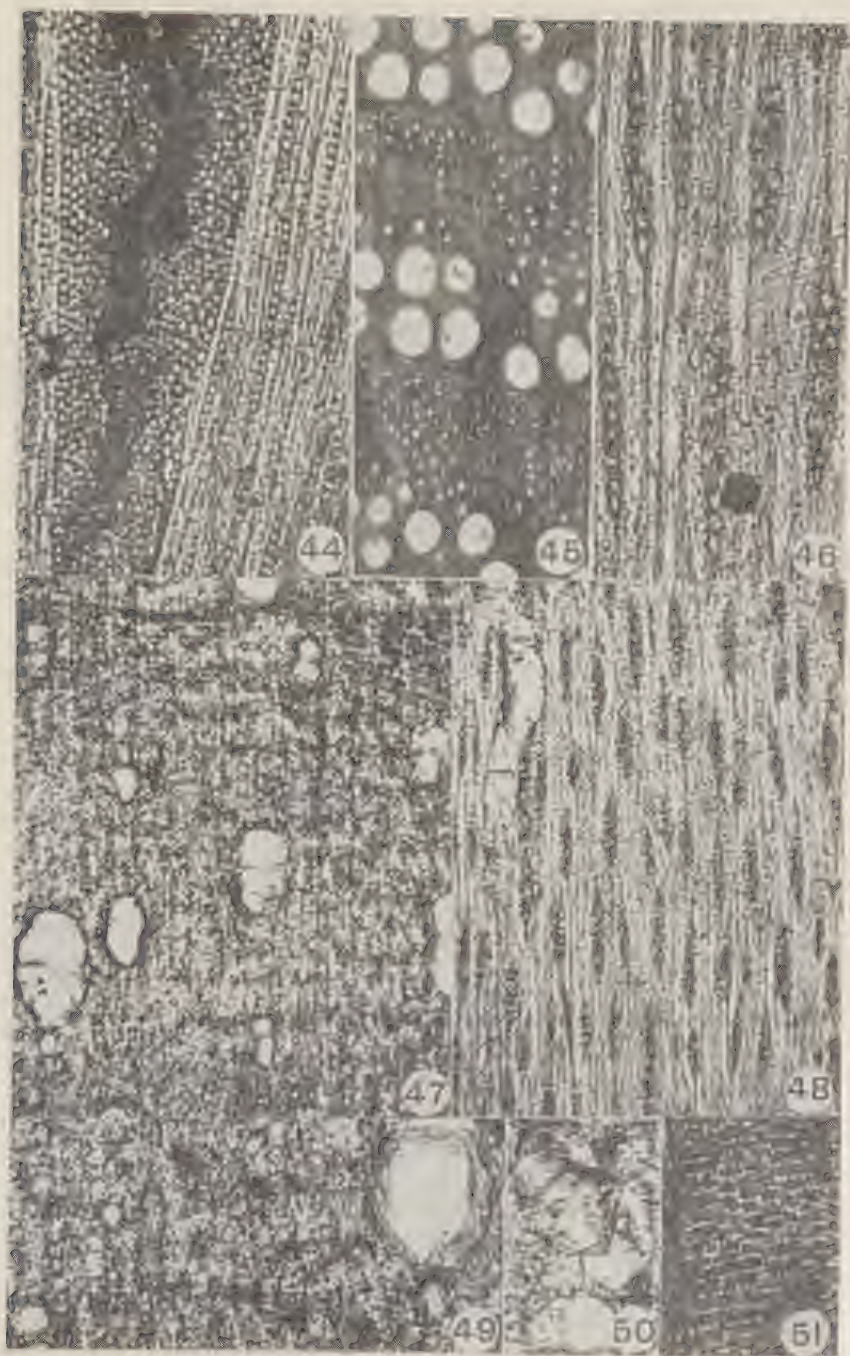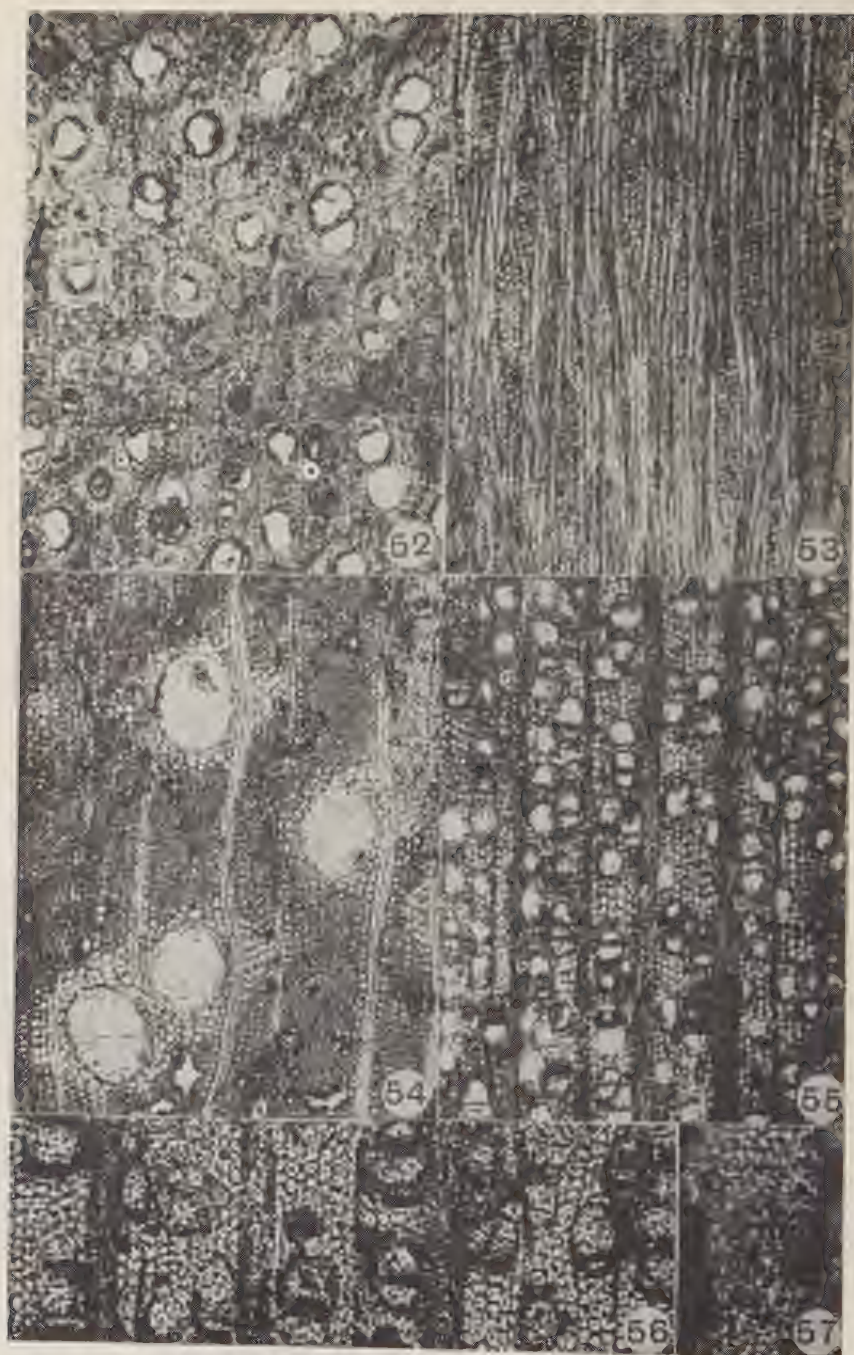
PRAKASH & BARGHOORN, MIOCENE WOODS

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PRAKASH & BARGHOORN, MIOCENE WOODS

THE GENERA OF TURNERACEAE AND PASSIFLORACEAE IN THE SOUTHEASTERN UNITED STATES *

George K. Brizicky

TURNERACEAE A. P. de Candolle, Prodr. 3: 345. 1828.
(Turnera Family)

Herbs or shrubs [rarely trees], usually pubescent. Leaves alternate, simple, toothed to entire [rarely pinnately divided], stipules small or absent. Flowers regular, bisexual, 5-merous, often heterostylous, axillary, solitary [or in terminal and/or axillary heads, racemes, cymes, or rarely panicles], typically 2-bracteolate. Floral tube (hypanthium) sometimes very short, deciduous after anthesis, often bearing 5 protuberances or glands just above the insertion of stamens and rarely a narrow, fringed corona within the petals. Sepals imbricate, on the rim of the floral tube. Petals distinct, perigynous, contorted in aestivation. Stamens 5, alternipetalous, usually inserted in the floral tube; filaments free; anthers introrse, dorsi-fixed near base, 2-locular at anthesis, dehiscing longitudinally; pollen grains ellipsoidal (prolate), mostly large, usually 3-colpate, reticulate. Gynoecium syncarpous, 3-carpellate; stigmas usually brushlike; styles 3, terminal, filiform, simple or dichotomously divided; ovary superior, sessile, 1-locular; placentae 3, parietal, each with 1 to numerous anatropous ovules with 2 integuments and thick nucellus [or placenta very rarely single, basal, uniovulate]. Capsule 1-locular, 3-valved, usually loculicidal and 3- to many-seeded [rarely septicidal and 1-seeded]; seeds with a membranace-ous, unilateral aril; seed coat alveolate-striate; endosperm fleshy; embryo large, axile, straight or slightly curved. Type genus: *Turnera* L.

A family of eight genera with about 120 species distributed primarily in tropical America (two genera, one exclusively, the other predominantly American, with about 100 species), in tropical Africa (six genera with about 17 species), Madagascar (two genera, one monotypic), and Rodriguez Island in the Mascarene group (one monotypic, endemic genus).

Diverse kinds of hairs (glandular and both simple and stellate non-glandular trichomes) which usually occur on the stems, leaves, pedicels, calyces, and fruits are of considerable taxonomic importance. Extrafloral nectaries are sometimes present at the base of the leaf blade ("basal glands") or on the petiole. The occasional occurrence of scalariform perforation plates in the secondary xylem (*Turnera Hindsiana* Benth.) or at least in the neighborhood of the primary xylem (*Turnera* spp., *Piriqueta* spp.) is noteworthy. Tanniniferous cells in leaves (epidermis) and primary cortex are of common occurrence.

The flowers of Turneraceae are recorded as ephemeral. According to Rao the floral tube ("calyx tube" or "hypanthium") is appendicular in nature, and the perigyny (in *Turnera*) has resulted from the adnation of the basal parts of sepals, petals, and stamens. A corona occurs only in *Piriqueta*. Almost 70 per cent of the species of the family have been recorded (by Urban) as having heterostylous flowers, the remaining having homostylous or (rarely) incompletely heterostylous flowers. In Turneraceae homo- and heterostyly seem to be characters of specific significance. Cross-pollination seems to be the rule, but, in homostylous and incompletely heterostylous flowers self-pollination (with self-fertilization) has been recorded in the case of failure of insect visitors, the withering corolla then bringing the anthers into contact with the stigmas. Bees have been reported as pollination agents in a few cases. The embryology of Turneraceae, studied in *Turnera ulmifolia*, essentially agrees with that of *Passiflora*. The germination power of seeds has been recorded (Urban) as lasting only a few years and as being low even in fresh seeds. No chromosome counts are known.

A close relationship of Turneraceae with Passifloraceae and Malesherbiaceae has been generally assumed by taxonomists. This view is supported by evidence from anatomy, palynology, and embryology (the last in regard to Passifloraceae). Malesherbiaceae seem to be a link between Turneraceae and Passifloraceae.

The family is of no economic importance.

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KEY TO THE GENERA OF TURNERACEAE

Peduncle distinct, flower pedicellate, ebracteolate; floral tube with a fimbriate corona in the throat just within the petals; styles more or less deeply divided; leaves without basal glands, stellate-hairy or glabrous. 1. *Piriqueta.*

Peduncle adnate to the petiole, flower sessile or subsessile, 2-bracteolate at base; corona absent; styles simple; leaves 2-glandular at base of blade, hairs simple. . . . . 2. *Turnera.*

1. **Piriqueta** Aublet, Hist. Pl. Guiane Fr. **1**: 298. 1775.

Erect herbs [rarely shrubs or trees], usually stellate-pubescent and often hirsute, rarely glabrous. Leaves alternate, petiolate or sessile, crenate or serrate (teeth often glandular or glanduliferous), rarely entire, exstipulate [rarely stipulate]. Inflorescences basically axillary and cymose (monochasial), often reduced to solitary flowers with a distinct peduncle jointed with the pedicel in the axils of upper leaves or bracts and forming bracted [or bractless] "racemes"; bracteoles absent or minute. Flowers heterostylous [or homostylous]. Floral tube turbinate or turbinate-campanulate, 10-ribbed, often with 5 fleshy liguliform or semiorbicular, cushion-like protuberances (extrastaminal nectaries) just above the insertion of the stamens. Sepals 5, on the margin of the floral tube. Petals 5, perigynous, cuneate or slightly unguiculate, yellow [or pink, purple, blue, or white]. Corona membranaceous, fringed, often inconspicuous. Stamens 5, filaments gradually broadened toward the base, inserted in the floral tube near its base; anthers ovate to oblong, usually obtuse or truncate at apex,

emarginate at base, the top often recurved after anthesis. Stigmas brush-like; styles 3, filiform, each more or less deeply dichotomously (rarely trichotomously) divided; ovary 1-locular, with numerous ovules on 3 parietal placentae. Capsule globose or ellipsoidal, smooth [or tuberculate], appressed-pubescent with simple hairs or glabrous, septicidal, 3-valved almost to the base; seeds numerous, straight or slightly curved, alveolate-striate; aril unilateral, crenate [to lacerate], as long as or shorter than the seed. TYPE SPECIES: *P. villosa* Aubl. (*P. cistoides* (L.) Griseb. var. *latifolia* Urb.). (Name derived from *piriquete*, the name of this plant in French Guiana.)

A genus of about 30 species, primarily of the American tropics, with its center of distribution in Brazil, but one species extending into the warmer temperate zone of eastern North America; in the Old World, three species in Madagascar and one in South Africa.

Only the South American–West Indian *P. caroliniana* (Walt.) Urb., a perennial herb with yellow, heterodistylous flowers, occurs in our area from the Florida Keys northward on the Coastal Plain to southwestern Georgia and eastern North Carolina. The species varies considerably in shape of leaves (obovate- or elliptic-oblong or lanceolate to narrowly linear) and pubescence of stems and leaves (stellate-tomentose and hirsute to stellate-hairy to glabrous). On this basis, five different varieties, four treated by Small (Man. Southeast. Fl.) as separate species, have been recognized in our area: var. *caroliniana*; var. *tomentosa* Urb. (*P. tomentosa* sensu Small, not HBK.); var. *glabra* (DC.) Urb. (*P. glabrescens* Small); var. *viridis* (Small) G. S. Torrey (*P. viridis* Small); and var. *exasperata* Urb. (*P. Tracyi* Gand.), the last differing from var. *glabra* only in the stellate pubescence of the leaves and perhaps included by Small in his *P. tomentosa*. Urban regarded *P. tomentosa* HBK., which does not occur in our area, as conspecific with *P. villosa* Aubl. and treated it as *P. cistoides* var. *latifolia*. The entire genus is much in need of a modern taxonomic revision, and field observations, culture experiments, and cyto-genetic studies are needed to determine the status (probably intraspecific) of the variants in our area. Our species is closely related to and very often confused with *P. cistoides*, which has approximately the same range in the West Indies and South America as *P. caroliniana*, but which differs mainly in the homostylous and somewhat smaller flowers.

Agents of seed dispersal are unknown, but myrmecochory appears probable.

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2.   Turnera Linnaeus, Sp. Pl. 1 : 271. 1753; Gen. Pl. ed. 5. 131. 1754.

Perennial [or annual] herbs, often woody at base, or shrubs [rarely trees], usually pubescent with simple [rarely stellate] hairs [or glabrous]. Leaves petiolate [or sessile], coarsely serrate [or crenate, rarely somewhat pinnately divided or entire], often 2-glandular at the base of the blade [or at the apex of the petiole], stipules minute or wanting. Inflorescences uniflorous in the axils of the upper leaves [rarely cymose or capitate], peduncles united with the petioles of subtending leaves [rarely free]. Flowers homostylous [or heterostylous], subsessile [or sessile], conspicu- ously 2-bracteolate at base. Floral tube cylindrical, broadened at apex [or hemispherical, campanulate, or turbinate], usually shorter than the sepals, sometimes bearing 5 alternipetalous semiorbicular projections above the insertion of stamens. Petals obovate, short-clawed, perigynous, yellow [more rarely pink, crimson, purple, blue, or white]. Stamens 5, inserted near the base of the floral tube, the lower parts of the filaments broadened and adnate by their membranaceous margins to the wall of the tube form- ing 5 nectar pockets; anthers narrowly ovoid-conical, acute at apex, emar- ginate at base. Stigmas brushlike [or fanlike]; styles 3, simple; ovary 1- locular, with numerous ovules on 3 parietal placentae. Capsule globose [or ovoid], verrucose [smooth or impressed-reticulate], hairy [rarely glabrous], rather thick-walled, 3-valved to below the middle [or to the base], the valves often recurved at apex. Seeds cylindric-clavate [or obovoid], straight or somewhat curved, alveolate-striate, glabrous [or puberulous], hilum often conspicuous, semiglobose [or conical]; aril whitish, lobed [crenate or lacerate], as long as or shorter than the seed. TYPE SPECIES: *T. ulmifolia* L. (Named in honor of William Turner, 1515– 1568, physician and herbalist, the "Father of English Botany.")

An entirely American genus of about 70 species occurring from Argentina to Texas. *Turnera ulmifolia*, a polymorphic species including about 12 varieties (six of which are heterostylous), is distributed throughout the range of the genus (except Texas). The West Indian var. *ulmifolia* (var. *angustifolia* Willd.) has been recorded as naturalized in our area on the Florida Keys and in peninsular Florida (and on the Coastal Plain from Florida to Louisiana, according to Small [Man. Southeast. Fl. 1933]). This variety and *T. subulata* J. E. Smith (*T. ulmifolia* var. *elegans* (Otto) Urb.) are now rather widely naturalized in the East Indies, Ceylon, Malaya, Indonesia, Seychelles, and Madagascar. Seed dispersal by ants has been recorded in both these species, and the other species of *Turnera* apparently are also myrmecochorous.

Dried leaves of *Turnera diffusa* Willd., of tropical America, Mexico, and Texas (here var. *aphrodisiaca* (Ward) Urb.), known as "damiana," have been used locally as a tonic and aphrodisiac. Infusions of leaves of *T.*

ulmifolia have been recorded as efficient against dysenteries on Java, while *T. opifera* Mart. has a similar reputation in Brazil; leaves of both are also utilized locally as tonics, expectorants, and/or astringents.

The genus is in need of a modern taxonomic revision.

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PASSIFLORACEAE Jussieu ex HBK. Nov. Gen. Sp. 2: 126. 1817, 'Passifloreae,'
(PASSION-FLOWER FAMILY)

Herbaceous or woody plants climbing by axillary tendrils [rarely erect, without tendrils]. Leaves alternate, simple [or very rarely compound], stipulate, petioles often with extrafloral nectaries (glands). Inflorescences axillary, bracteate, cymose (di- or monochasial), usually associated with a terminal or collateral tendril, sometimes reduced to geminate or solitary 1-flowered peduncles. Flowers regular, bisexual [rarely unisexual], 5[4, rarely 3]-merous, complete, rarely apetalous. Sepals and petals imbricate, perigynous; the floral tube usually with a "corona." Stamens 5[–10], alternipetalous, hypogynous, free from the gynophore or raised on an androgynophore, anthers versatile, 2-locular at anthesis, longitudinally dehiscent. Gynoecium 3[–5]-carpellate; stigmas capitate, clavate, or discoid; styles 3 [or 1–5]; ovary stipitate, rarely sessile, 1-locular, with numerous anatropous ovules on 3[–5] parietal placentae. Fruit a berry [or capsule]; seeds arillate with straight embryo and fleshy endosperm. TYPE GENUS: *Passiflora* L.

A primarily tropical family composed of 12 genera with over 500 species discontinuously distributed over a considerable part of the tropical zone. Eight of the genera (five monotypic) are restricted to the Old World, three (*Dilkea, Mitostemma,* and *Tetrastylis*) are exclusively American, and one (*Passiflora*) is preponderantly New World.

The presence of a "corona" (in combination, however, with the usually climbing habit, the cymose inflorescences associated with tendrils, the stipitate ovary, and the arillate seeds) is perhaps the most outstanding feature of the family. Absent only in *Machadoa* and two (of six) sections

of *Adenia*, the "corona" occurs in all the other members of Passifloraceae. In its simplest form (*Adenia, Crossostemma, Tetrapathaea*) it consists of a membrane or a ring of threads, situated at the rim of the floral tube; in the most complex form (*Passiflora* and *Tetrastylis*) it is composed of many series of threads, membranes, folds, etc. This complexity requires a special descriptive terminology for the various parts of the "corona," which differ in appearance and/or size, position in the floral tube, and biological function. The terminology used by Killip (based on Harms) in his monograph of the family is followed here. The following subdivisions of the "corona" are generally recognized: the *corona* (sensu stricto), *operculum, nectar ring* or *annulus,* and *limen.* (See illustration.)

Passifloraceae are closely allied with Turneraceae, Malesherbiaceae, and Flacourtiaceae–Paropsieae. Some relationship with Cucurbitaceae through Achariaceae is also presumed by some taxonomists. A close affinity with Caricaceae appears somewhat questionable. In its present delimitation, based mainly on biological characters (e.g., climbing habit) and gross morphology of the flowers, the family appears to be fairly natural. There are, however, some evidences from the wood anatomy and palynology which suggest a taxonomic re-evaluation of Passifloraceae and their closest allies (especially Flacourtiaceae–Paropsieae), based on data from comparative anatomy and other botanical disciplines. Our knowledge of the family as a whole in regard to the cytogenetics, embryology, and floral anatomy is rather limited, being almost exclusively based on studies on a relatively small number of species of *Passiflora.*

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1. **Passiflora** Linnaeus, Sp. Pl. 2: 955. 1753; Gen. Pl. ed. 5. 410. 1754.

Herbaceous or woody vines [rarely erect herbs, shrubs, or small trees]. Leaves alternate, simple [rarely compound], predominantly 3–5-nerved from the base, undivided or more frequently palmately [2]3–5-lobed, entire or toothed, petiolate, the petiole often glanduliferous, stipules setaceous to broadly ovate, sometimes foliaceous, entire, toothed or deeply cleft, usually persistent. Tendrils axillary, simple. Inflorescences axillary, usually reduced to solitary or paired 1-flowered (rarely 2–10-flowered) peduncles, sometimes flowers fascicled [or arranged in dichasial or raceme-like inflorescences]. Bracts (bract and bractlets) usually present, small and scattered or relatively large (sometimes foliaceous) and verticillate, forming an involucre near the base of the flower. Floral tube patelliform, cupuliform, funnelform, or campanulate [sometimes short- or long-tubular], rounded or impressed at base. Sepals 5, membranaceous or subcoriaceous, often more or less petaloid, sometimes dorsally appendaged (corniculate, etc.) just below the apex. Petals 5, membranaceous, delicate, greenish, white or highly colored, as long as or shorter than the sepals, usually situated at the margin of the floral tube just within the sepals [rarely attached below the mouth of the floral tube], sometimes absent. Corona of 1 to several series of distinct or more or less united processes, sometimes high colored and/or variegated in various shades [rarely membranaceous]; operculum borne within or below the corona, membranaceous, flat or plicate, entire, dentate or fringed, [sometimes filamentous, rarely absent]; nectar ring within or below the operculum, sometimes absent; limen borne at or above the base of the androgynophore or encircling the base of sessile ovaries, sometimes absent. Stamens 5, usually raised on an androgynophore, filaments free, attached to the back of the anthers near their middle; anthers linear to oblong, at first introrse, appressed to the sides of the ovary, extrorse when mature; pollen grains large, globose to ellipsoid, reticulate, 3–12-colpate. Gynoecium syncarpous, borne on an elongated gynophore, very rarely sessile or subsessile; styles usually 3, distinct or united at the base, cylindric or clavate, each with a capitate or reniform stigma; ovary 1-locular, usually with 3 parietal placentae, each with 2–4 rows of 2-integumented ovules with a thick nucellus. Fruit a small to very large, ovoid, ellipsoidal or globose berry; seeds several to many, covered by a fleshy aril open only at the apex, ± laterally compressed, oblong to suborbicular in outline, with an outer thin, mem-

branaceous sarcotesta, and an inner hard, reticulate or transversely grooved sclerotesta; endosperm fleshy, embryo with a straight radicle and flat, foliaceous cotyledons. LECTOTYPE SPECIES: *P. incarnata* L.; see Britton & Brown, Ill. Fl. No. U. S. ed. 2. 2: 565. 1913. (Name from Latin, *passio* (*Christi*), passion or sufferings of Christ, and *flos*, flower, applied from a fancied resemblance of its parts to the implements of crucifixion.) — PASSION-FLOWER.

A genus of about 400 species, primarily of the American tropics, represented in the Western Hemisphere by about 360 species, most of the remaining species occurring in tropical Asia, a few in Australia, Melanesia, and Polynesia, and one on the Mascarene Islands. Harms (1925) subdivided the genus into 21 sections; Killip, however, arranged the American species in 22 subgenera. Six or seven species, representing four subgenera, are indigenous to our area.

Subgenus APODOGYNE Killip (woody vines, petioles 2-glandular, flowers small, in fascicles of 3–6, bracts small, borne near base of peduncle, floral tube patelliform, corona filamentose in two series, operculum plicate, ovary sessile, fruits small, seeds transversely sulcate) includes only *P. multiflora* L., with unlobed, pinnately or subtriplinerved leaves and an anomalous stem structure. The species is mostly West Indian in range (Greater Antilles [except Jamaica] and the Virgin Islands), extending northward on the Florida Keys (Key West to Elliott's Key) to southern peninsular Florida.

Subgenus PLECTOSTEMMA Masters (herbaceous vines, petioles with or without glands, flowers small, peduncles solitary or in pairs, usually 1 (rarely 2–10)-flowered, bracts small, scattered [in ours] or wanting, floral tube patelliform [or campanulate], petals sometimes wanting, corona filamentous, in 1 or 2 series, operculum plicate, ovary on a gynophore, fruits small, seeds reticulate or transversely sulcate) includes about 115 species, three of which are indigenous in our area. The very polymorphic *P. suberosa* L. (*P. pallida* L.), $2n = 24$, with undivided to deeply 3-lobed leaves and apetalous flowers, is common throughout tropical America (except the Guianas), and is widely naturalized in the Old World tropics. It occurs on the Florida Keys and in peninsular Florida as far north as the Indian River (Brevard County) in the east, and the mouth of Tampa Bay in the West; it also reaches southernmost Texas (Cameron County). An autotriploid chromosomal race ($2n = 36$) which appeared spontaneously in the wild diploid race has been found by Storey (1950) in Hawaii. *Passiflora sexflora* Juss., with 3-lobed leaves (which often appear almost 2-lobed because of reduction of the middle lobe), glandless petioles, and geminate 2–10-flowered peduncles, is West Indian–Central American in range. It is disjunct southward in Colombia and reaches our area on the Everglade Keys in southern Florida. *Passiflora lutea* L., $2n = 24, 84$, the most northerly of the genus, is distributed throughout our area, extending beyond it westward to Texas, Oklahoma, and Kansas, and northward to southern Illinois, Indiana, Ohio, and Pennsylvania. Recorded chromosome

FIG. 1. **Passiflora.** a–j, *P. incarnata*: a, portion of stem with fruits, × ¼; b, summit of petiole with glands, × 3; c, bud with bractlets, × 1; d, bractlet with glands, × 5; e, flower, color pattern omitted, × 1; f, flower, central portion in partial vertical section, two stamens, one style-arm removed, × 2 — note 1-sepal, 2-petal, 3-outer corona, 4-inner corona, 5-operculum, 6-limen; g, ovary, diagrammatic cross section, × 6; h, very young seed with developing aril, × 3; i, older seed with aril, × 3; j, seed with sarcotesta removed, × 4.

counts "indicate that polyploidy exists in this species and suggest that there are intraspecific chromosomal races" (Baldwin). The South American *P. morifolia* Mast. has been reported as naturalized near Clemson, South Carolina (Small, Man. 896. 1933, as *"P. Warmingii* Mast."). The likewise South American *P. gracilis* Jacq. ex Link, $2n = 18, 20$, was introduced into South Carolina (Abbesville County) in the past century.

Subgenus PASSIFLORA (subg. *Granadilla* (Medic.) Mast.) (herbaceous [rarely woody] vines, petioles 2-glandular, flowers generally large and highly colored, solitary or in pairs in the leaf axils, bracts entire or serrulate [or serrate], often large, forming an involucre near the base of the flower, floral tube campanulate to short-tubular, corona filamentous in 3 to several series, operculum nonplicate, ovary stipitate, fruit usually large, seeds reticulate) includes about 100 species, predominantly South Ameriman, two in our area. *Passiflora incarnata,* $2n = 18$, with deeply 3–5-lobed glandular-serrulate leaves and large flowers with corniculate sepals and lavender (pink or white) corona, is distributed throughout our area, extending westward to Texas, Oklahoma, and southeastern Kansas, northward to the southern parts of Missouri, Illinois, Indiana, and Ohio and southwestern Pennsylvania; it is introduced and naturalized in Bermuda. The fruits, "maypops," are ellipsoidal, greenish yellow, 3.5–6.0 cm. long; the arils of the seeds ("pulp" of fruits?) are edible. The species is often cultivated elsewhere as an ornamental. *Passiflora pallens* Poepp. ex Mast., with 3-lobed entire-margined leaves, conspicuous foliaceous stipules, large white flowers, and sepals with a foliaceous appendage on the back just below the apex, is known in our area only from a few localities in Dade and Monroe counties in southern peninsular Florida. *Passiflora caerulea* L., $2n = 18$, probably indigenous to Brazil, Uruguay, and Paraguay, is the commonest passion-flower grown as an ornamental in- and/or out of doors in both hemispheres. Artificial hybrids between this and several other species are known. *Passiflora edulis* Sims, *P. laurifolia* L., *P. maliformis* L., and *P. quadrangularis* L. (including *P. macrocarpa* Mast.), all $2n = 18$, are extensively cultivated in the tropics for their edible fruits and/or as ornamentals.

Subgenus DYSOSMIA (DC.) Killip (herbaceous vines [or erect shrubs or subshrubs], often with glandular hairs, petioles glandless, stipules usually pinnately cleft or parted, flowers medium-sized to large, bracts pinnatifid to tripinnatisect with filiform gland-tipped segments, floral tube campanulate, corona in 4 or 5 series, operculum nonplicate, fruits medium-sized, seeds reticulate) comprises about 15 species distributed from Brazil to Mexico and the West Indies. *Passiflora foetida* L., $2n = 18, 20, 22$, an extremely polymorphic species including 38 varieties (Killip 1938), ranges throughout the New World tropics, extending as far north as Arizona (var. *arizonica* Killip) and Texas (var. *gossypiifolia* (Desv.) Mast., $2n = 20$). In our area the species (var. *riparia* (C. Wright) Killip) apparently is known only from Fruitland Park, Lake County, Florida, where it was collected by R. N. Jones in 1920. Killip includes "Southern Florida" in the natural range, but the single collection from central Florida suggests

an introduction. The species has been introduced into the tropics of the Old World, where it is now completely naturalized and widely distributed. The unripe fruits are poisonous. [The exclusively South American subg. ASTROPHEA (DC.) Mast. is noteworthy, for, in addition to vines, it also includes tendrilless trees (e.g., *P. arborea* Spreng.) and shrubs (e.g., *P. gigantifolia* Harms).]

The occurrence in the wood of fibriform vessel elements in *Passiflora* (and in some Flacourtiaceae–Paropsieae) presents a notable anatomical peculiarity. The anomalous stem structure of *P. multiflora* probably occurs in some other members of the genus and the family.

Anatomical studies indicate that the floral tube (floral cup) in *Passiflora* is of appendicular origin (except the very base, which is receptacular), involving the fusion of the basal portions of sepals and petals. According to Masters and Puri, the sepals probably are homologous with leaf sheaths, and the dorsal appendages of the sepals (corniculi and the like) are homologous with petioles. The corona and operculum are also appendicular, being outgrowths of the inner wall of the floral tube; the limen, however, probably is staminodial in nature. The parietal placentae of the ovary apparently have been derived from ancestral axile placentae.

Little is known regarding the pollination agents in *Passiflora*, but the following are considered the most probable: bees and other small hymenopters (for subg. PLECTOSTEMMA, sects. *Cieca* and *Decaloba*), large bumblebees, carpenter bees, and large moths (for subg. PASSIFLORA, CALOPANTHUS, DISTEPHANA, and GRANADILLASTRUM), lepidopters (for some species of subg. ASTROPHEA), and hummingbirds (for some species of subg. ASTROPHEA and perhaps subg. TACSONIA and PSILANTHUS, which have long cylindrical floral tubes). Cross-fertilization seems to be the rule, although occasional self-fertilization has been recorded in *P. gracilis*. Self-fertilization is at least in some cases prevented by androgyny (recorded in *P. caerulea* and *P. lutea*, but probably more frequent within the genus) and/or self-sterility (in *P. caerulea*, *P. edulis*, and several other species); *P. mollissima* (HBK.) Bailey, $2n = 18$, is self-fertile.

In the bud both stamens and styles are upright, the anthers being introrse and parallel to the filaments. During anthesis the filaments spread out, taking first a horizontal position, but soon curving down; at the same time the anthers turn around their place of attachment about 90°, becoming perpendicular to the filaments, and finally horizontal and extrorse. Almost simultaneously with the movement of the stamens (or later in protandrous flowers) the styles recurve, and the stigmas are brought to or above the level of the anthers and between them. In this position both anthers and stigmas can be brushed by the back of insect visitors.

Chromosome numbers have been counted in about 20 species, several forms, and five interspecific hybrids. All the species examined (except perhaps *P. foetida*) fit within a polyploid series for which a basic number of six or three has been suggested. (See Storey.) Interspecific hybrids are almost invariably sterile.

The leaves and/or stems, sometimes roots, more rarely fruits and/or

seeds of many species contain various amounts of hydrocyanic acid (cyanogenetic glucoside), and several species are recorded as or suspected of being poisonous, e.g., *P. alba* Link & Otto, *P. caerulea*, *P. Herbertiana* Ker-Gawl. ("pulp" of the fruits strongly cyanogenetic), etc. In *P. alba* another toxic substance, perhaps a toxalbumin, seems present in addition to the hydrocyanic acid. *Passiflora alata* Dryander (subg. *Passiflora*) and its allies contain the bitter (?) principles maracugin (maracujin) and passiflorin. Many species have been recorded as having medicinal properties (antispasmodic, sedative, tonic, anthelmintic, diuretic, emetic, etc.) and are locally used in medicine. Various species are of domestic importance as ornamentals and/or for edible fruits (cf. subg. PASSIFLORA).

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A STUDY OF HYBRIDIZATION IN DOWNINGIA
(CAMPANULACEAE)

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Every taxonomic study is tentative, and none is to be regarded as final, for each is, instead, one more laborious step toward a greater understanding of living organisms. Each careful investigation provides a new level from which subsequent workers may move forward in the analysis of the complexities and the synthesis of the information about a taxonomic group. Progression is thus by stages in taxonomy, as in other branches of science, although this seems often to be misunderstood by workers in other fields, and perhaps sometimes even by taxonomists. The genus *Downingia* Torr., a western American group of Campanulaceae–Lobelioideae, comprising about a dozen species of small, semiaquatic annuals with colorful, intricately formed corollas, well illustrates this continuing development.

The first species of *Downingia* was described in 1829 from plants grown from seeds collected by David Douglas in what is now Oregon, but only this and one other species were recognized until 1886. Then, from 1886 to 1895, nine new species were described, largely by E. L. Greene, who studied the genus in the field. Subsequently, in 1922, W. L. Jepson published a revision of the species of *Downingia* in California, recognizing only seven, and, in 1937, R. F. Hoover provided a key to the species in that state, including thirteen.

Eventually, in 1941, one hundred and twelve years after the description of the first species, came the first monographic study, that of Rogers McVaugh, which represents a masterful achievement in blocking out the species of *Downingia* on morphological bases. Working entirely from herbarium materials, in which the characteristic details of form and color-pattern of the corolla are largely obscured, it was necessary for McVaugh to treat the genus "exactly as if it were a genus of grasses or of the Compositae, where the distinguishing features are often technical ones and equally often invisible to the unaided eye." This admirable monograph may be modified in details, but the basic alignments will stand. Later (1943), McVaugh himself reduced one species to varietal status. His taxonomic treatment has been followed by Mason (1957), who provided excellent illustrations of most of the taxa, and by Munz and Keck (1959).

With McVaugh's monograph as a firm foundation, the present study was undertaken in the hope of adding something of the biological nature of the species, their chromosome numbers and genetic relationships, and the nature of the interspecific barriers. Annual, easily cultivated in quantity in a small space, with handsome and characteristic corollas, convenient for hybridization studies, and with a manageable number of well-marked species, *Downingia* offers almost as many advantages for a study of living

plants as it does disadvantages in an herbarium study. Begun in California, most of this work has been carried out in greenhouses in Massachusetts and North Carolina with restricted samples of only eight of the species and with no possibility for further field observations. However, the results confirm the taxonomic treatment of McVaugh and show the existence of a pattern of aneuploidy and of strong genetic incompatibilities between species. Since the pressure of other matters has made it impossible to carry this research further, it is presented here, with full recognition of its limitations and gaps, to clear the way for other workers who will undoubtedly solve many more problems, while posing still others. None of these studies of *Downingia* has been complete and final, but each is a step toward the continuing taxonomic goal of knowledge and understanding of plants.

METHODS

The first collections studied were made in California in the spring of 1949 by friends at the University of California or by myself, and a few hybridizations between wild plants brought into the greenhouses at Berkeley were tried at that time. Subsequently, a number of botanists kindly collected and forwarded seeds of various species. Attempts were made to grow and observe the crosses made in 1949, as well as other available collections, at the Biological Laboratories, Harvard University, Cambridge, Massachusetts, in the spring of 1950 and again in 1951. In the next three years, plantings at the University of North Carolina, Chapel Hill, were successful only in 1953; those in 1952 and 1954 mark unfortunate breaks in the data, for all failed, almost none of the seeds germinating (for causes unknown).

Seeds of *Downingia* were sown in February in 3-inch pots or 6-, 7-, or 9-inch azalea pots or bulb pans, in a more or less standard sand-soil-compost mixture. The sifted, firmly packed soil was covered with a thin layer of very fine soil on which the minute seeds were either scattered or placed

individually. A light dusting of sifted soil was added and the surface lightly tamped. The pots stood in saucers or pans of water and were kept constantly wet.

A large number of plants of *Downingia* can be grown in a single pot, allowing ready comparison within small populations. Under such conditions, individual plants do not reach the size or vigor which may be seen under favorable conditions in the wild or when grown singly in the greenhouse, but limitations of space necessitated the arrangements adopted.

In Cambridge six hours of additional light from two 1000-watt bulbs suspended over the greenhouse bench were used in 1951. The effect of the supplemental light will be seen under each species in the length of time required for flowering in this year in comparison with 1950 and 1953.

Sandwiched between other more pressing work, chromosome counts could not always be made at the proper time and were not obtained for all of the collections grown. The counts recorded, all meiotic, showed a pattern of aneuploidy from 11 pairs to 12 and to 10, 9, and 8. These chromosome numbers are given under the species concerned and are summarized in the crossing diagram and discussion toward the end of the paper. Meiosis occurred when the apparent flower bud (not including the pedicel-like ovary) was about 1 mm. long. The best results were obtained when the first buds were being produced in a population; at that time it was possible, with a little patience over a period of a few days, to obtain satisfactory meiotic material. Later on, after the plants were larger, I found it difficult to select buds which were of the proper age.

The material gave good results with a modified Carnoy's fixative (4 parts chloroform: 3 absolute ethyl alcohol: 1 glacial acetic acid) and proprionocarmine. Slides were made permanent with a modification of Bradley's vapor transfer method (Stain Tech. **23**: 41–44. 1948). Documenting herbarium specimens are in the Gray Herbarium.

The pollen discharge device of *Downingia* (see below) makes hybridization relatively easy. The ovary of a flower was held between forefinger and thumb and the anther tube grasped carefully with forceps and tweaked off. In most instances a clean separation from the filament tube could be obtained and the anthers pulled away, leaving the protruding style with the rudimentary stigmas. When the stigmas matured, pollination of the emasculated flower was accomplished easily with a spear-pointed needle which was used to depress the anther bristles and to collect the out-pouring of pollen. Pollen was then transferred to the appropriate stigma, the needle dipped in 70 per cent alcohol, the pollinated flowers marked with jeweler's tags, and the fruits allowed to mature. (Since the bright yellow pollen is rather powdery, some stray contamination may have come about through the methods used, for the small size of the plants, their closeness in the pots, and the importance of the ovary in the photosynthesis of the plant all precluded any sort of hermetic bagging. Such seedlings were easily recognized in interspecific crosses but could be a serious source of error in crosses involving races of a species. Nonhybrid seedlings of this kind are given for each of the interspecific crosses.) In *Downingia cuspi-*

data and *D. bicornuta* var. *bicornuta* the capsules tended to dehisce almost immediately upon maturity, necessitating prompt gathering. In other species most capsules on a single plant could be gathered at the same time and placed in individual coin envelopes. Each capsule involving an inter-specific cross was split lengthwise with a needle and the number of seeds and/or the condition of aborted ovules recorded.

More than 900 cross-pollinations were effected between the species assembled, the seeds sown, and the results tabulated. These are summarized under each of the species and in *figure 13*, which shows all crosses attempted and the several categories of results, as well as chromosome numbers.

GENERAL OBSERVATIONS

The twelve species of *Downingia* are all low annuals admirably adapted to the climatic conditions of the western United States, especially that part in which the Mediterranean type of climate, with its wet, cool winters and hot, dry summers, prevails. All are associated with moisture, and most are plants either of vernal pools or vernally wet soils. Growth is slow during the winter. With lengthening days, rising temperatures, and drying of the vernal pools, the rate of growth increases and the plants come rapidly into flower and set and mature seeds before the drying of the soil kills the parental plant. Numerous minute, fusiform seeds (to 150 or more) are borne on axile or parietal placentae in elongate 1- or 2-locular cylindrical capsules, which in some species (e.g., *D. cuspidata*) open almost immediately upon maturity by longitudinal splits, but in others (e.g., *D. ornatissima*) appear to be almost or quite indehiscent. In spite of their small size the seeds of some species, particularly those of habitats with the hottest, driest summers (e.g., *D. concolor, D. cuspidata, D. ornatissima, D. pusilla*) appear to be relatively drought resistant and may retain their germinability over a period of years. Those of cooler and moister habitats (e.g., *D. montana, D. yina* var. *major, D. elegans*) appear to be viable a much shorter length of time.

In nature, the seeds presumably germinate in fall or winter, either on wet soil or under water. The seedling shows an adaptation characteristic of a number of aquatics or plants of seasonally wet habitats. (Cf. *Drosera, Sarracenia, Pinguicula*, and many aquatics illustrated in W. C. Muenscher, Aquatic Plants of the United States [1944].)

In about five to seven days (in the greenhouse), the hypocotyl pushes out of the micropylar end of the seed and comes into contact with the soil. The radicle remains quiescent until the development of a ring of long root hairs at the base of the hypocotyl provides an anchoring attachment. The radicle then begins to grow, and, as the primary root elongates, the usual root hairs are formed.

The hypocotyl then elongates, becoming upright and green. The linear-lanceolate cotyledons gradually emerge, but remain pressed together, the tips being held within the seed coat. With the beginning of growth of the

plumule, the cotyledons may expand or may be held together permanently by the seed coat. Under favorable conditions growth proceeds rapidly. As with many marsh or aquatic plants, the stems are equipped with large gas channels which extend into the roots. Axillary branches may occur from the cotyledons upward, and adventitious rooting may occur at the nodes. A burst of growth appears in connection with the formation of the flower buds, which are solitary and sessile in the axils of bractlike leaves (the first appearing in the axil of the fifth to tenth or fifteenth leaf above the cotyledon, depending upon the species). These upper leaves and especially the elongated cylindric ovaries (which may easily be mistaken for pedicels) must account for much of the photosynthetic area of the plant.

In culture, flowering may occur in *D. pusilla* (the most reduced species) in about 35 days from the time of planting, or in about 45–56 days in most species, or may require some 70 in *Downingia bicornuta* var. *bicornuta*. The flowers are inverted in anthesis by tortion of the ovary, the apparent lower lip being morphologically the upper one. The flowers, with their elaborate and colorful corollas, obviously are adapted to insect pollination. The "lower" lip is more or less highly modified as a "landing platform" and is marked with characteristic patterns of blue to violet, white, yellow to green, and dark purple. The androecium is equally specialized, reserving the pollen until activated by an insect visitor. Most of the species (with the exception of the diminutive *Downingia pusilla* which seems to be self-pollinated) are normally outcrossing, but are self-compatible and may, under some circumstances (see below), be self-pollinated. Seedlings obtained from self-pollination in *D. insignis* and *D. pulchella* show variation in color pattern, suggesting the heterozygosity associated with outcrossing. No evidence of apomixis was found in the present investigation, and none of the cultures set seeds without pollination.

Androecium. The androecium of *Downingia* is a characteristic and highly specialized one, modified along the same lines as that of many of the members of Campanulaceae–Lobelioideae and resembling especially those of its nearest relative, *Porterella carnulosa* (Hook. & Arn.) Torr. (see Mason, 1957, *fig. 344*), and of *Isotoma axillaris*, described recently by Melville (1960). The five stamens are united around the style, the filaments forming a tube and the five anthers a more or less cylindric anther tube oriented at various angles to the filament tube. (See *figs. 1, 8*; also McVaugh, 1941, *figs. 1–3, 5, 6, 10*, and Mason, 1957, *figs. 331–340*.) The three larger anthers are uppermost, the tips curving downward and inward to those of the two shorter and smaller lower anthers and forming a mouth-like opening. Each of the two smaller anthers is tipped by a few forwardly directed short hairs and by a conspicuous flexible, flan-like bristle which projects forward at the base and then usually downward. The bases of the two bristles and the tuft cover the opening between the anthers, preventing the loss of pollen which is shed inwardly into the common cavity of the anther tube. When one or both of the bristles are

FIG. 1. Stamens of species of *Downingia*, in lateral view to show differences in size, angle of anther tube to filament tube, and length and position of anther bristles. Numerals following the name refer to populations listed under the species. All figures × 6 or 12. a–c, *D. bicornuta* var. *bicornuta* (30); d, e, *D. bicornuta* var. *picta* (40); f, *D. bicornuta* var. (2674), diagrammatic; g, h, *D. concolor* var. *concolor* (34); i, j, *D. cuspidata* (31); k, l, *D. elegans* var. *brachypetala* (39); m, n, *D. insignis* (14); o, p, *D. ornatissima* var. *ornatissima* (36); q, r, *D. ornatissima* var. *eximia* (28); s, t, *D. pulchella* (26).

pushed backward by a pollinator, the opening is uncovered and a quantity of powdery pollen bursts forth in a stream, dusting the insect. Subsequent displacements produce additional quantities of pollen.

The impetus for the pollen movement is provided primarily by the growth of the style. At the time of shedding of the pollen, the style is about as long as the filament tube, but the two stigmatic lobes are rudimentary and are tightly appressed to each other, the two occupying about the same diameter as the style. Immediately behind them is a ring of several ranks of stylar hairs. With the continuing elongation of the style, the hairs act as a plunger, putting the pollen ahead under pressure and pushing it against the tips of the three upper stamens, so that it pours out, as though a valve were opened, when the anther bristles are depressed. A second source of pressure on the pollen may possibly come from the shrinking and drying of the tough outer walls of the anthers. The growth of the style continues, and, when the undeveloped stigmatic lobes push through and beyond the anther tube, they expand rapidly, separating, recurving, and maturing. (See Mason, 1957, *fig. 334f.*)

The flowers are thus strongly proterandrous, and self-pollination usually cannot occur. Exceptionally, however, in all of the species studied here, the style may fail to push through the anther tube, with the result that the stigmas expand within the tube and self-pollination occurs. In the single collection grown of *Downingia pusilla*, self-pollination of this type appeared to be the rule, for the stigmas were seldom seen to protrude from the anther tube, and, in contrast to the other species, in greenhouse culture plants of *D. pusilla* always set many seeds whether or not artificial pollination was attempted. (Apomixis, with the possible exception of pseudogamy, may be ruled out here, for emasculated flowers of *D. pusilla* did not set seeds.)

In his monograph of *Downingia*, McVaugh found that the androecium furnishes some of the most useful taxonomic characters for the identification of herbarium specimens (in which the corollas are almost always deformed and faded). Although flower size may vary greatly with the size and vigor of the plant, the androecium is relatively constant quantitatively and has a characteristic range in length. It is usually distinctive in shape of the anthers, the angle of anther tube to filament tube, the anther pubescence, the length and shape of the bristles, and the degree of exsertion of the anthers from the corolla tube. Such characteristics, combined with the elaborately formed and colored corollas, suggest specific pollination agents, or at least different sizes of agents. However, only a single field observation is available. (See *Downingia concolor*.)

The pollen discharge device of *Downingia* is more advanced than that of *Lobelia* and some other Lobelioideae in the elaboration and specialization of the two trigger bristles, the bases of which close the anther tube. In several species of *Lobelia* in which I have tested this mechanism, the bristles are lacking and the opening is closed by the two tufts of forwardly directed hairs which also act as the trigger device, releasing the pollen when pushed downward. In the eastern United States, the ruby-throated

hummingbird regularly trips the device of *Lobelia cardinalis* and may be seen with the top of the head yellow with pollen, while honey bees visiting *L. siphilitica* deliberately manipulate the discharge hairs and collect and carry away in their pollen baskets the bluish-gray pollen with which they are then dusted. However, the bristles of *Downingia* and *Porterella* would seem to make for a somewhat more efficient and sensitive mechanism.

OBSERVATIONS ON THE SPECIES

The data given here include notes which have accumulated in the course of growing and attempting to hybridize the eight species. For ease in consultation, the species are arranged in alphabetical order. Under each will be found observations (intended only to supplement those of McVaugh [1941] and the excellent drawings in Mason [1957]) on color patterns and morphology of the flowers, documenting data on the collections grown, summaries of the crosses attempted with other species, chromosome counts, and miscellaneous notes and comments which bear on the biology or taxonomy of the species. In all crosses the seed parent is given first. The hybrids of *Downingia insignis* and *D. pulchella* are treated separately in a following section.

Downingia bicornuta Gray var. bicornuta

FLOWER MORPHOLOGY AND COLOR: See *fig. 2* for conformation and general color pattern of corolla; see also McVaugh (1941, *figs. 4, 5*, and p. 27), Mason (1957, p. 755). Lower lip of corolla nearly plane, not concave as in var. *picta*, the outer portion blue-violet (Bradley's violet [Ridgeway]), the central area white with two green to sulfur-yellow spots (these usually confluent as single patch) extending to the mouth of the corolla tube; upper lobes erect or reflexed, divergent or overlapping, blue-violet without and within; corolla tube blue-violet, darker on the upper side, the lateral walls with or without violet veining (this inconspicuous on account of the darker ground color); lower side of tube blue-violet within two-thirds of way from base, then with two elongated green or yellow spots or streaks (these visible on the outside) banded with reddish purple at either end, then with a band of violet, and finally with a deep violet band across the front of 2 of 4 hornlike projections at the mouth of the tube, the deep violet sometimes extending into the tube; hornlike projections shorter than in var. *picta*, erect and not curving outward. Corolla tube 5–6.1 mm. long from base to upper sinus, (3.8–)4.8–6.2 mm. long to lateral sinus in fresh material (*vs.* 2.5–4.5 mm. in dried material studied by McVaugh). Anthers not exserted from corolla tube or only tip exserted; anther tube not at an angle to filament tube; anther bristles twisted, short, 0.6–1.5 mm. long. (See *fig. 1a–c.*)

COLLECTION GROWN: 30, from Boggs Lake, Lake Co., Calif., *Estella Leopold*, 31 May 1949 (plants pollinated in wild, seeds matured in greenhouse).

CROSSES ATTEMPTED:

30 × *D. concolor* (34, 87): 133 seeds from 5 capsules, 77 white or pale green lethals, 21 nonhybrids; reciprocal, 65 seeds from 25 capsules, 2 white lethals, 45 nonhybrids.

30 × *D. bicornuta* var. *picta* (40): 620 seeds from 9 capsules, green and vigorous hybrid seedlings flowering in about 56 days (1953); reciprocal (20 capsules, seeds not counted) equally successful; F_1 apparently fertile but F_2 lost in 1954.

30 × *D. ornatissima* (28, 36): 14 seeds from 6 capsules, 2 white lethals, 6 nonhybrids; reciprocal (27, 28, 36 × 30), 235 seeds from 20 capsules, 15 white lethals, 62 nonhybrids.

30 × *D. cuspidata* (33): 3 seeds from 4 capsules, 1 nonhybrid; reciprocal, seeds aborted near maturity, did not germinate or were lethal (in 33 × 30, no seeds from 15 capsules; but 105 seeds from 1 capsule gave 18 nonhybrid seedlings; in 31 × 30, 175 seeds from 7 capsules, about one-half of these planted, 16 white or yellowish lethals, 26 nonhybrids).

30 × *D. pulchella* (26): 49 seeds from 5 capsules, no hybrids, 38 nonhybrids; reciprocal, 21 seeds from 10 capsules, no hybrids, 29 nonhybrids.

30 × *D. insignis* (14): 13 seeds from 4 capsules, no hybrids, 12 nonhybrids; reciprocal, 79 seeds from 13 capsules, no hybrids, 38 nonhybrids.

30 × *D. elegans* var. *brachypetala* (39): 8 seeds from 3 capsules, no hybrids, 1 nonhybrid; reciprocal, 24 seeds from 12 capsules, no hybrids, 1 nonhybrid.

CHROMOSOMES: $n = 11$ (metaphase, anaphase II) in population 30; meiosis regular.

Plants developed relatively slowly, beginning to flower in 69 days in 1950, 64–70 days in 1951. The flowers were without the curious odor of var. *picta*. This collection is the rather large-flowered, slow-maturing northern plant which extends from California into Oregon, Nevada, and Idaho.

Hybrids between vars. *bicornuta* and *picta* were green, vigorous, and apparently quite fertile, beginning to flower in 56 days in 1953. The color pattern of the corolla was like that of var. *bicornuta*, but the corolla tube was shorter and the anther bristles longer. An F_2 planted in 1954 failed, along with all other seeds planted that year. See also var. *picta* below.

Downingia bicornuta var. picta Hoover

FLOWER MORPHOLOGY AND COLOR: See *fig. 2* for conformation and general color pattern of corolla; see also McVaugh (1941, *fig. 6* & p. 27), Mason (1957, *fig. 335a, b*). Outer portion of concave lower lip of corolla violet, central area white with a central yellowish-green spot; upper lobes reflexed or erect, violet, paler at the base; corolla tube conspicuously reticulate within, with deep violet veins on a paler background, the upper side of the tube usually greenish or brownish for a distance of about 1–1.5 mm.; lower side of corolla tube zoned with purple at base, white with two green lines in the median portion, and purple at the distal end, the purple extending onto 4 hornlike projections at the mouth of the tube; exterior

of corolla tube light reddish purple (much paler than in var. *bicornuta*), the reticulations conspicuous, the tube often greenish distally; hornlike projections longer and more conspicuous than in var. *bicornuta*, curving outward, purple, the two central darker because of the extension of the greenish-yellow patch in center of lip over them. Corolla tube 2.4–3.1 mm. long from base to upper sinus, 2.0–2.9 mm. long to lateral sinus (vs. 1.5–2.6 mm. at lateral sinuses in dried material studied by McVaugh). Anthers usually exserted from corolla tube for almost the full length of the anther tube; anther tube at an angle to filament tube. (See *fig. 1d,e*.)

COLLECTIONS GROWN:

40, from 2 mi. n. of Sheldon, Sacramento Co., Calif., *G. L. Stebbins, Jr.*, 20 May 1950 (seeds).

46, from 3.5 mi. n. of Snelling on La Grange Road, Merced Co., Calif., *R. C. Bacigalupi*, 22 April 1951 (seeds).

CROSSES ATTEMPTED:

40 × *D. bicornuta* var. *bicornuta* and reciprocal: good seed-set, green and vigorous hybrids of intermediate morphology. (See var. *bicornuta* above.)

40 × *D. concolor* var. *concolor* (34): 22 seeds from 2 capsules, no hybrids, 11 nonhybrids; reciprocal, 61 seeds from 14 capsules, 7 yellowish lethals, 13 nonhybrids.

40 × *D. ornatissima* (28, 42): 26 seeds from 5 capsules, no hybrids, 10 non-hybrids; reciprocal (with 27, 28, 36, 42), 214 seeds from 25 capsules, 7 white lethals, 35 nonhybrids.

40 × *D. cuspidata* (29, 31): 6 seeds from 2 capsules, none germinating; reciprocal (with 31), 397 seeds from 9 capsules, 78 white or very pale green lethals, 106 nonhybrids.

40 × *D. insignis* (14): not attempted; reciprocal, 18 seeds from 5 capsules, no hybrids, 10 nonhybrids.

40 × *D. elegans* var. *brachypetala* (39): 13 seeds from 6 capsules, no hybrids, 5 nonhybrids; reciprocal not attempted.

CHROMOSOMES: $n = 11$ (metaphase I, anaphase I, metaphase II) in population 40; meiosis regular.

Plants developed rapidly, the first flower bud located in the axil of the fifth leaf above the cotyledons, meiosis occurring in about 36 days and flowering in 50 days in 1951, 53 days in 1953, the first flowers opening two weeks ahead of var. *bicornuta* (cf. McVaugh, 1941, pp. 28, 30). The flowers had a strong "mousy" odor quite different from that of var. *bicornuta* or any of the other species grown.

The flowers of *Downingia bicornuta* var. *bicornuta* and var. *picta* are so different, when seen on the living plant, that on morphological grounds one could well deduce that two species are involved. The corollas differ in color pattern, shape of the lobes and length of the tube, and the androecia in length, angle of anthers to filament tube, degree of exsertion of anthers, and length of the paired twisted bristles. In addition, var. *picta* begins to flower earlier, an adaptation probably related to its restriction to the Central Valley of California. However, on the basis of the twisted bristles,
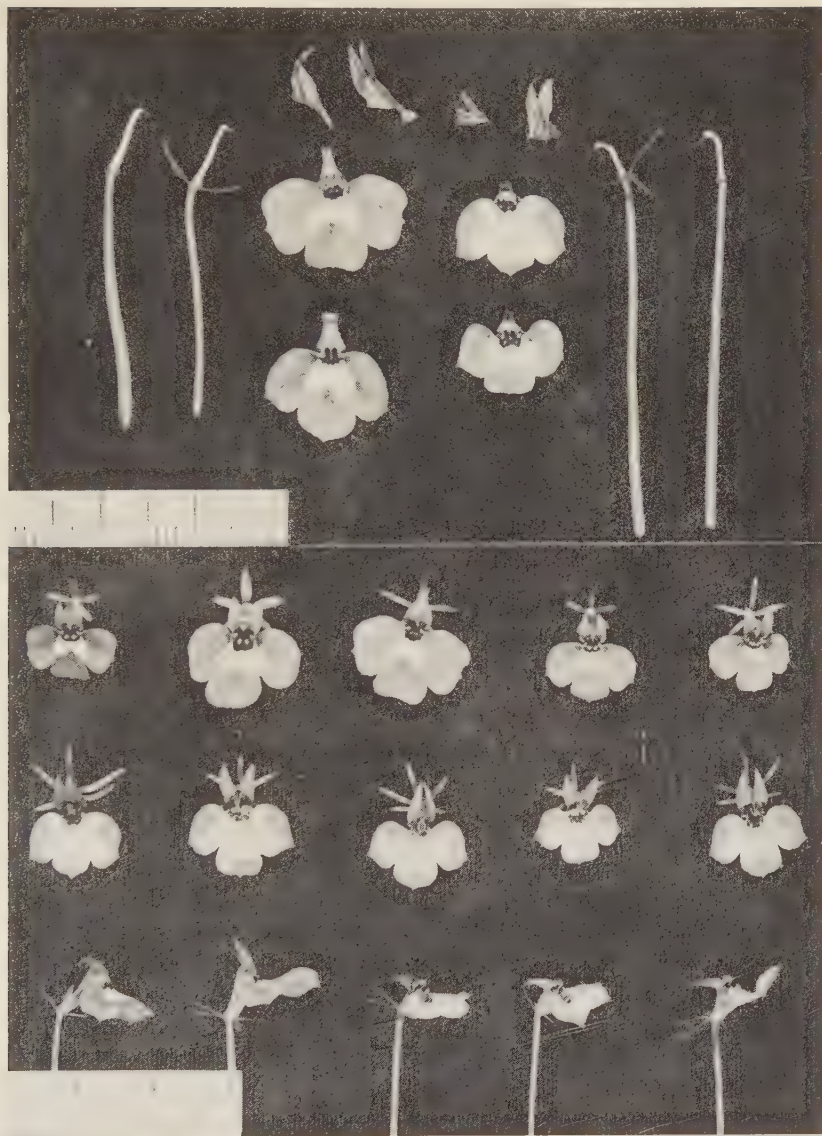
Fig. 2. Flowers of *Downingia bicornuta* vars. *bicornuta* and *picta*. Above: left, var. *bicornuta*, androecium and portion of ovary, upper corolla lobes, lower corolla lobes; right, var. *picta*. Below: top row, var. *bicornuta*; center row, var. *picta*; bottom row, two flowers of var. *bicornuta* (left), three of var. *picta*.

the corolla tube bearded within on the lower side, and the four conspicuous hornlike projections on the lower lip at the entrance to the corolla tube, as well as the occurrence of occasional apparent intermediates in the Sacramento Valley where the ranges of the two appear to overlap, Mc-Vaugh treated both as components of one species. The chromosome numbers and crossing evidence are entirely in accord with this disposition.

Downingia bicornuta var. [with short anther bristles and corolla tube]

FLOWER MORPHOLOGY AND COLOR: Appearing to be a small-flowered form of var. *bicornuta*; sepals and formation and color pattern of corolla as in var. *bicornuta*, but the corolla tube somewhat paler. Corolla tube short, 3.0–4.5 mm. long from base to upper sinus, 2.7–4 mm. long to lateral sinus in fresh material. Anthers as in var. *bicornuta*, with short, straight or twisted bristles, the anther tube not exserted from the corolla tube and not at an angle to the filament tube; filament tube ca. 2.6 mm. long. (See *fig. 1f.*)

COLLECTION GROWN: in alkaline pools, 2 mi. w. of Tranquility Junction on State Highway 180, Fresno Co., Calif., *Bacigalupi, Wiggins & Ferris 2674*, 29 July 1941 (GH) (flower and fruit).

CROSSES ATTEMPTED: This collection was crossed with vars. *picta* (46) and *bicornuta* (30) in 1953. Seed-set apparently was normal, but the hybrid seed planted in 1954 failed, along with all other seeds sown that year.

CHROMOSOMES: $n = 11$ (metaphase–anaphase I); meiosis regular.

The seeds from which this culture was grown came from a then ten-year-old specimen in the Gray Herbarium. The seeds, which bore faint longitudinal cellular markings, germinated readily in about 8 days. The plants developed rapidly, meiosis occurred about 34 days after sowing and flowering began in about 55 days in 1951 (sown in mid-April) or 50 days in 1953 (sown in late February).

This plant, which indicates the need for further study of variation in *Downingia bicornuta*, is undoubtedly closely allied to var. *bicornuta*, which it resembles in the conformation and coloration of the corolla, in the sepals, in the included anthers, in the straight filament-anther tube, and in the short anther bristles. It differs, however, in the short corolla tube (intermediate in length between the cultures grown in vars. *bicornuta* and *picta*), the filament tube (even shorter than that of var. *picta*), and in the time of flowering. It thus combines some features of vars. *bicornuta* and *picta*, but the uniformity of the population grown, the short filament tube, and the short bristles suggest at least that this is not of immediate hybrid origin. The geographical distribution remains to be determined, but it may be suspected of being a low-altitude, rapidly maturing form of at least the southern part of the Central Valley of California. Collections from the Central Valley which appear to be var. *bicornuta* should be examined critically.

This collection was determined by McVaugh as *Downingia bella* Hoover, a species which was imperfectly known to him and one of which I have seen only scanty herbarium material. (See Mason, 1957, p. 754, for illustration of *D. bella*.) The determination is easily understandable, for, in the herbarium specimen, the details of the corolla are quite obscured and the anther bristles are not the characteristically twisted ones of *D. bicornuta*. However, whatever the identity of *D. bella*, a plant which McVaugh thought to be related to *D. concolor*, the present plant is clearly allied to *D. bicornuta*, with both of the recognized varieties of which it is presumably interfertile.

Downingia concolor Greene var. concolor

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, *fig. 12* & pp. 18–21), Mason (1957, pp. 752, 755). Corolla pale to bright blue, the lower lip with a central white area and, at the mouth of the corolla tube, with a 2-lobed to w-shaped to almost square velvety, dark-violet spot covering two low ridges, each of which sometimes bears a streak of yellow within the mouth of the tube; white of the lip sometimes reduced or lacking, the whole lip then blue, the purple spot then completely obscuring the yellow streaks; corolla tube narrowly funnel-shaped, the lower side reddish violet from base to middle (or the entire length in dark flowers), the distal portion light blue to almost white.

COLLECTIONS GROWN:

15, from dry, hard adobe, roadside ditch, ca. 10 mi. s. of Dixon, Solano County, Calif., *C. E. Wood 7614*, 16 April 1949 (plants in flower; growing with *D. insignis*).

20, in vernal pools in meadow, ca. 2¼ mi. ne. of Middletown, Lake Co., Calif., *C. E. Wood 7620*, 28 April 1949 (plants in flower).

34, from near Dixon, Solano Co., Calif., *M. Nobs*, May 1949 (living plants).

87, a population originated in the greenhouse through crossing of 15 × 20 in May, 1949, before any chromosome numbers had been determined.

1170, growing in Middletown Meadow (Skaggs Ranch or Bar X Ranch), 3 mi. e. of Middletown on Highway 53, Lake Co., Calif., *A. R. Kruckeberg*, 2 July 1949.

INTERSPECIFIC CROSSES ATTEMPTED:

34, 87 × *D. ornatissima* (27, 35, 36, 42): 47 seeds from 28 capsules, 1 white lethal, 25 nonhybrid seedlings; reciprocal (27, 28, 35, 36 × 34, 87), 129 seeds from 35 capsules (43 from 1 capsule, 23 from another), 14 white lethals, 52 nonhybrids.

34, 87 × *D. bicornuta* var. *bicornuta* (30): 65 seeds from 25 capsules, 2 white lethals, 45 nonhybrids; reciprocal, 133 seeds from 5 capsules, 73 white to pale green lethals, 22 nonhybrids.

34 × *D. bicornuta* var. *picta* (40): 61 seeds from 14 capsules, 7 very pale, yellowish lethals, 13 nonhybrids; reciprocal, 22 seeds from 2 capsules, no hybrids, 11 nonhybrids.

15, 34, 87 × *D. cuspidata* (29, 31, 33): 37 seeds from 23 capsules, 4 pale green
   lethals, 22 nonhybrids; reciprocals (31, 33 × 15, 20, 34, 87), 188 seeds from
   27 capsules, 30 white lethals, 64 nonhybrids.

34 × *D. pusilla* (2063): 71 seeds from 2 capsules, 48 weak and nearly white
   lethals, some surviving almost 4 weeks.

15, 20, 34, 87 × *D. pulchella* (25, 26): 27 seeds from 18 capsules, no hybrids,
   17 nonhybrids; reciprocal (25, 26 × 15, 34, 87), 86 seeds from 16 capsules,
   1 white lethal, 67 nonhybrids.

34, 87 × *D. insignis* (14): 32 seeds from 21 capsules, no hybrids, 25 nonhybrids;
   reciprocal (14 × 15, 20, 34, 87), 131 seeds from 40 capsules, 3 white or
   very pale green lethals, 45 nonhybrids.

34 × *D. elegans* var. *brachypetala* (39): 99 seeds from 9 capsules, no hybrids,
   90 nonhybrids; reciprocal, 34 seeds from 5 capsules, no hybrids, 28 non-
   hybrids.

CHROMOSOMES: $n = 8$ (metaphase II) in population 34; $n = 9$ (late diakinesis
to metaphase I) in population 1170; meiosis regular in both.

Plants matured rapidly, flower buds appearing in the axil of the seventh
leaf above the cotyledons. Meiosis occurred in about 33 days after plant-
ing in 1951, and the first flowers opened in 55 days in 1950, 43–49 days in
1951, and 53 days in 1953.

The presence of two chromosome numbers (eight and nine) in two
populations (34, 1170) of this species in northern California is of special
interest. The meiotic behavior of a hybrid between these two races should
provide a valuable clue to the way in which aneuploid repatterning of the
chromosome complement has proceeded in the genus. Chromosome counts
were not obtained on cultures 15 and 20 which are from approximately the
same areas as are the 8- and 9-chromosome cultures (34 and 1170 respec-
tively) and which might well have the same number of chromosomes as
those collections. Wild plants from which cultures 15 and 20 were derived
were crossed in California in 1949, long before any chromosome counts had
been made. The resulting population (87) appeared to be fully fertile, and
estimates, confusing at the time, of nine (definite) and eight (tentative)
were both obtained, but these data are anything but unequivocal. No
meiotic irregularities were seen, and one count of 1000 pollen grains showed
98.1 per cent stainable.

Another relationship which should be investigated is that of *Downingia
concolor* var. *brevior* McVaugh, known only from San Diego County, Cali-
fornia, and distinguished by its shorter and readily dehiscent capsules, to
these more northern plants. Also of interest is the relationship of *D. con-
color* to *D. bella* Hoover, which it resembles in a number of features.

This is the only species in which I have observed pollination in the wild.
In Lake County, California, a small bee, unfortunately not captured, was
seen visiting successive flowers (population 20). Pollen was being ejected
on the face of the bee above the mouthparts, suggesting that the positions
of the anthers in the various species may result in the deposition of pollen
on specific parts of the pollinator's body.

Downningia cuspidata (Greene) Greene ex Jepson

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, p. 31), Mason (1957, p. 759). Lower lip of corolla nearly plane, the lobes sky-blue to pale blue (or the blue varyingly restricted, in some plants only the very tips bluish), occasionally violet or pink (or anthocyanin sometimes entirely suppressed), the central area white with a two-lobed yellow spot covering two inconspicuous, low, mound-like ridges at the entrance to the corolla tube; upper lobes correspondingly blue, violet, or pink, usually somewhat darker than lower lobes, erect; corolla tube narrow, pale, unmarked, except for the tip of the yellow spot which extends to within the entrance; mouth of corolla tube narrow, mostly filled by the slightly exserted anther tube.

COLLECTIONS GROWN:

29, in one of four vernal pools about 1.5 feet deep with bare (dry) bottom and scattered plants of *Eryngium*, ca. 2 mi. e. of Keystone, Tuolumne Co., Calif., *C. E. Wood 7629 & C. T. Mason*, 9 May 1949 (only this species present, in fruit; absent in two shallower adjoining pools).

31, in very dry, very hard clay in three dry vernal pools in blue-oak grassland, ca. 3 mi. w. of Coarse Gold, Madera Co., Calif., *C. E. Wood 7631 & C. T. Mason*, 10 May 1949 (most plants with mature seeds, a few, including one pink and one violet, in flower).

33, in vernal pools along highway in bottomlands near a creek, ca. 1.2 mi. w. of Chinese Camp, Tuolumne Co., Calif., *C. E. Wood 7633 & C. T. Mason*, 10 May 1949 (fruiting in a dry pool, but flowering in wet areas).

47, from 3 mi. n. of Snelling on La Grange Road, Merced Co., Calif., *R. C. Bacigalupi*, 22 April 1951 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

31, 33 × *D. concolor* var. *concolor* (15, 20, 34, 87): 188 seeds from 27 capsules, 30 white lethals, 64 nonhybrids; reciprocal (29, 31, 33 × 15, 34, 87), 37 seeds from 27 capsules, 4 pale green lethals, 22 nonhybrids.

31, 33 × *D. ornatissima* (27, 35, 36): 536 seeds from 33 capsules, 136 white lethals, 78 nonhybrids; note especially 31 × 27, 293 seeds from 6 capsules, 112 white lethals, 48 nonhybrids; reciprocal (with 27, 28, 35, 36), 27 seeds from 41 capsules, no hybrids, 10 nonhybrids.

31, 33 × *D. bicornuta* var. *bicornuta* (30): seeds aborted near maturity, did not germinate or were white lethals (in 33 × 30, no seeds from 15 capsules, but 105 seeds in one capsule gave 18 nonhybrid seedlings; in 31 × 30, 175 seeds from 7 capsules, about one-half of these planted, 16 white or yellowish lethals, 26 nonhybrids); reciprocal (33 × 30), 3 seeds from 4 capsules, no hybrids, 1 nonhybrid.

31 × *D. bicornuta* var. *picta* (40): 397 seeds from 9 capsules, 78 white or very pale green lethals, 106 nonhybrids; reciprocal (40 × 29, 31), 6 seeds from 2 capsules, none germinated.

31 × *D. pusilla* (2063): 39 seeds from 2 capsules, no hybrids, 20 nonhybrids; reciprocal (with 29, 31), plants not emasculated, 61 seeds from 5 capsules, no hybrids, 47 nonhybrids, two capsules, each with 25 flat and twisted seeds aborted near maturity.

31, 33 × *D. pulchella* (26): 117 seeds from 20 capsules, 5 white or pale green lethals, 33 nonhybrids; reciprocal (26 × 29, 31, 33), 85 seeds from 37 capsules, 1 white and 9 very pale green lethals, 62 nonhybrids.

31, 33 × *D. insignis* (14): 104 seeds from 24 capsules, 3 white lethals, 14 non-
    hybrids; reciprocal, 78 seeds from 17 capsules, 1 yellowish lethal, 40 non-
    hybrids.
31 × *D. elegans* var. *brachypetala* (39): 38 seeds from 2 capsules, no hybrids,
    11 nonhybrids; reciprocal (29 × 39), 12 seeds from 11 capsules, no hybrids,
    11 nonhybrids.

CHROMOSOMES: $n = 11$ in population 29 (metaphase I, anaphase II), in popu-
lation 33 (metaphase I, metaphase II), and in population 47 (diakinesis, meta-
phase II, anaphase II); meiosis quite regular throughout.

Seeds sown in February germinated readily, and the plants flowered in
45 days in 1951, 48–52 days in 1953. However, seeds sown at Cambridge
on Dec. 8, 1949, and cultivated without supplemental light required 80–90
days, with growth proceeding very slowly through the first two months.
The first flower bud appeared in the axil of the fifth leaf above the cotyle-
dons. The flowers had a delicate fragrance reminiscent of that of *Syringa
vulgaris*.

The hyaline lines on the ovary, which mark the valves of the capsule,
are quite conspicuous in the living plant, even being reddish in color in
some individuals. The prompt dehiscence of the capsule necessitates special
care in harvesting seeds.

The form of the corolla and its lack of purple spots, the capsule splitting
at maturity, and the seeds with spiral cellular markings on the seed coat,
all features stressed by McVaugh, are characteristic. Although I have seen
the species growing only in Tuolumne and Madera counties, California, it
was evident there (and from the cultures subsequently grown) that the
amount (intensity) and distribution of anthocyanin in the corolla varies
greatly both within and between populations. Crosses between populations
from this region (29, 31, 33) resulted in good seed-set and green, vigorous
seedlings. McVaugh's disposition of *Downingia pallida* Hoover (described
from adjoining Stanislaus County) as a synonym of *D. cuspidata* is un-
doubtedly the correct one.

The interspecific data show the strong genetic barriers characteristic of
other species of the genus. However, it is noteworthy that when *Downingia
cuspidata* is used as the seed parent in crosses with *D. bicornuta* vars.
bicornuta and *picta*, *D. ornatissima*, and *D. concolor*, albino seedlings are
produced, whereas the reciprocal crosses usually fail even to set seeds. A
single count of 1000 pollen grains from a plant of population 31 showed
99.3 per cent stainable grains.

Downingia elegans var. brachypetala (Gandoger) McVaugh

FLOWER MORPHOLOGY AND COLOR: See *fig. 3* for conformation of corolla
and general color pattern; see also McVaugh (1941, p. 55). Corolla tube
broadly funnelform, the lateral sinuses much deeper than the dorsal, the
two upper lobes reflexed, often divergent; lower lip concave, about equalling
the upper lobes in length, merging gradually with the tube, the three lobes
parallel; corolla light blue, the tube pale without, the lower lip with a cen-

tral area of white, lacking ridges or yellow spots in the throat; lower side of corolla tube within pale, with an ill-defined, more or less diffuse bluish-violet spot on either side of the bluish-violet midvein (other veins sometimes bluish violet and visible through the corolla).

COLLECTION GROWN: 39, from the Calapooya River, Linn Co., Oregon, *L. Constance*, 5 Aug. 1950 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

39 × *D. concolor* var. *concolor* (34): 34 seeds from 5 capsules, no hybrids, 28 nonhybrids; reciprocal, 99 seeds from 9 capsules, no hybrids, 90 nonhybrids.

39 × *D. ornatissima* (36, 42): 11 seeds from 6 capsules, 1 pale green (probably nonhybrid); reciprocal (with 28, 36), 80 seeds from 16 capsules, no hybrids, 43 nonhybrids.

39 × *D. bicornuta* var. *bicornuta* (30): 24 seeds from 12 capsules, no hybrids, 1 nonhybrid; reciprocal, 8 seeds from 3 capsules, no hybrids, 1 nonhybrid.

39 × *D. bicornuta* var. *picta* (40): not attempted; reciprocal, 13 seeds from 6 capsules, no hybrids, 5 nonhybrids.

39 × *D. cuspidata* (29): 12 seeds from 11 capsules, no hybrids, 11 nonhybrids; reciprocal (with 31), 38 seeds from 2 capsules, no hybrids, 11 nonhybrids.

39 × *D. pulchella* (26): 38 seeds from 9 capsules, no hybrids, 20 nonhybrids; reciprocal, 37 seeds from 10 capsules, no hybrids, 14 nonhybrids.

39 × *D. insignis* (14): 23 seeds from 10 capsules, no hybrids, 11 nonhybrids; reciprocal, 30 seeds from 9 capsules, no hybrids, 11 nonhybrids.

CHROMOSOMES: $n = 10$ (metaphase II) in population 39; meiosis regular.

FIG. 3. Flowers of *Downingia elegans* var. *brachypetala* (top row and bottom row, right) and of *D. insignis* (center row and bottom row, left).

Seeds sown at the end of February, 1951, grew through a relatively long vegetative period. The first buds appeared in the axil of the tenth to fifteenth leaf above the cotyledons in about 45 days, meiosis occurred in about 50 days, and the first flowers opened in about 60 days. Seedlings of this species were easily distinguished from all others· grown by the lanceolate, completely entire leaves.

This plant appears to represent *Downingia elegans* var. *brachypetala*, with which it agrees in respect to conformation of corolla and stamens (*fig. 1k*) and habit. It does not have, however, the two yellow spots in the white area on the lower lip which are characteristic of var. *elegans*. The chromosome number ($n = 10$) is distinctive, and, in addition, the plant is completely isolated genetically from the seven other species grown: in no instance was it possible to obtain hybrid seeds in interspecific crosses. In view of these results, McVaugh's suggestion (1941, p. 41) of a hybrid origin for atypical specimens of *Downingia elegans* collected with *D. insignis* (Malheur Co., Oregon, *Cusick 1261* [F]) appears to be an unlikely possibility. The developmental differences between the unilocular ovary with parietal placentation and the bilocular ovary with axile placentation would also seem to be such incompatible ones that hybrids between these species could hardly be expected.

Although this collection of *Downingia elegans* var. *brachypetala* was the only representative which was studied in any detail of the species which are characterized by unilocular ovaries with parietal placentation, it was possible to grow a few plants of *D. yina* var. *major* McVaugh (*D. willamettensis* M. E. Peck), from Corvallis, Benton Co., Oregon, in the spring of 1955. In the latter plants, which began to flower in 68 days, the corolla tube was slender (ca. 5 mm. long), the upper lobes erect, and the anther tube not at an angle to the filament tube. The lower lip was concave, as in *D. elegans* var. *brachypetala*, and the corolla markings were similar, with two light purple dots in the mouth of the corolla tube and no yellow markings on the lip. McVaugh (1941, p. 57) found anomalous collections of var. *brachypetala* which seemed to combine features of *D. yina* var. *major* and suggested that "it is not impossible that var. *brachypetala* is of hybrid origin." Certainly further study of the group composed of *D. montana* Greene, *D. yina* Applegate vars. *yina* and *major*, and *D. elegans* vars. *elegans* and *brachypetala* is in order. Regardless of their interrelationships, however, it is probable that these five taxa with unilocular ovaries comprise a distinctive genetic, as well as morphological, group within the genus.

Downingia insignis Greene

FLOWER MORPHOLOGY AND COLOR: See *figs. 3, 7* for conformation and general color pattern of corolla; note broadly funnelform throat, parallel, ascending upper lobes (with an angle of 20–50° between them), concave lower lip which is not at an angle to the tube; see also McVaugh (1941, p. 40), Mason (1957, p. 749). Corolla sky-blue (to violet-blue, probably sometimes pink or white), the veins darker, the lower lip with a central

white area; white area with two triangular-oblong green or yellow-green spots each extending onto a low fold which ends in a yellow protuberance at the mouth of the corolla tube; green and yellow spots interrupted by a dark violet-purple bandlike spot across each of the folds, the two spots often with diffuse color between or confluent as a band and truncating the central white area; corolla tube within with midveins of the three lower corolla lobes with violet streaks from base to mouth and with 6 or more small reddish-violet spots near the mouth (2 flanking each of the yellow protuberances), a streak of reddish violet extending downward from each spot. See also *figs. 1, 7* (as well as McVaugh, 1941, *fig. 1*; Mason, 1957, *fig. 332c* [*332d* is not characteristic]) for androecium.

COLLECTIONS GROWN:

14, from dry, hard adobe, roadside ditch, ca. 10 mi. s. of Dixon, Solano Co., Calif., *C. E. Wood 7614*, 16 April 1949 (in flower; growing with *Downingia concolor*).

44, on eastern outskirts of Stockton along State Highway 4, San Joaquin Co., Calif., *R. C. Bacigalupi*, 21 April 1951 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

14 × *D. concolor* var. *concolor* (15, 20, 34, 87): 131 seeds from 40 capsules, 3 white or very pale green lethals, 45 nonhybrids; reciprocal (with 34, 87), 32 seeds from 21 capsules, no hybrids, 25 nonhybrids.

14 × *D. ornatissima* (27, 35, 36): 75 seeds from 28 capsules, no hybrids, 65 nonhybrids; reciprocal (with 27, 28, 36), 35 seeds from 22 capsules, 2 white lethals, 1 greenish yellow, 26 nonhybrids.

14 × *D. bicornuta* var. *bicornuta* (30): 79 seeds from 13 capsules, no hybrids, 38 nonhybrids; reciprocal, 13 seeds from 4 capsules, no hybrids, 29 nonhybrids.

14 × *D. bicornuta* var. *picta* (40): 18 seeds from 5 capsules, no hybrids, 10 nonhybrids; reciprocal not attempted.

14 × *D. cuspidata* (31, 33): 78 seeds from 17 capsules, 1 yellowish lethal, 40 nonhybrids; reciprocal, 104 seeds from 24 capsules, 3 white lethals, 14 nonhybrids.

14 × *D. pulchella* (25, 26): See below. Abundant seed-set, hybrids very pale green, weak, many inviable, others slow-growing, but if flowering, fertile; F_2 partially lethal, backcrosses to either parent vigorous and fertile.

14 × *D. elegans* var. *brachypetala* (39): 30 seeds from 9 capsules, no hybrids, 11 nonhybrids; reciprocal, 23 seeds from 10 capsules, no hybrids, 11 nonhybrids.

CHROMOSOMES: $n = 11$ (metaphase II) in population 14; meiosis regular.

Seeds planted in February germinated readily, the plants flowering in 51–55 days in 1950, 46–52 days in 1951, and 54-55 days in 1953. Pollen 94.0 to 99.7 per cent stainable. (See TABLE I.)

Although *Downingia insignis* was long confused with *D. elegans*, McVaugh pointed out the numerous differences between the two species and correctly oriented the relationships of *D. insignis* toward *D. pulchella* instead. With *D. laeta* (Greene) Greene (of which I have not seen living
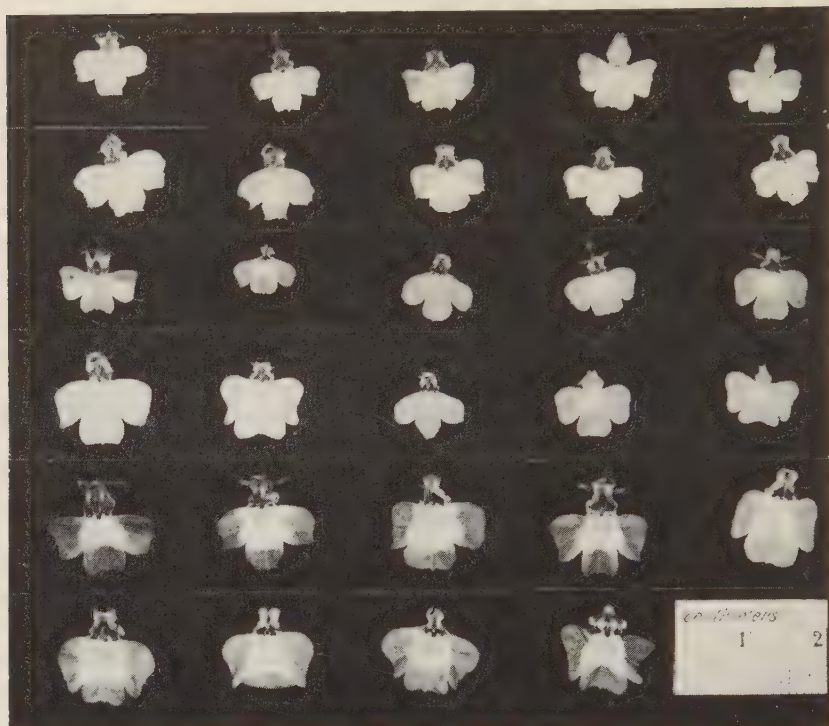
Fig. 4. Flowers of three populations of *Downingia ornatissima* to show geographical variation. Two top rows: Population 35 (var. *ornatissima*), from Tehama County, California. Two center rows: Population 41, from Sacramento County. Two bottom rows: Population 27 (var. *eximia*), from Stanislaus County, California.

material) the two form a group of morphologically related species with strong genetic incompatibilities with other species of the genus, although the chromosome numbers and crossing data show more of a relationship to other species with bilocular ovaries (*D. bicornuta, D. concolor, D. cuspidata, D. ornatissima,* et al.) than to those with unilocular ovaries (*D. elegans* var. *brachypetala,* et al.). The large, concave lower lip not forming an angle with the broadly funnelform corolla tube, the striking color pattern, and the anther tube at right angles to the long filament tube suggest pollination by some fairly large bee.

Downingia ornatissima Greene

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, p. 23), Mason (1957, p. 753). Corolla deep blue, violet-blue or violet to pale lilac or nearly white (with only the tips of the lower lobes tinged with blue), with a squarish white central area with two greenish-yellow to bright yellow
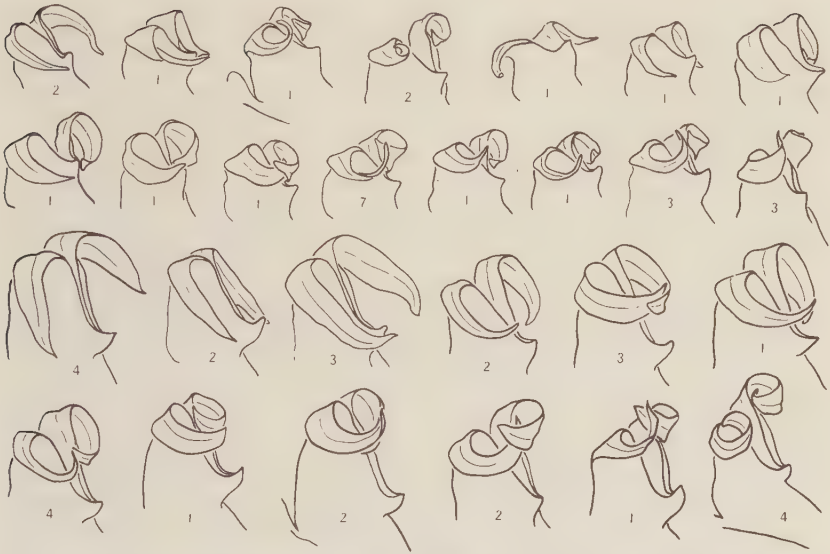
FIG. 5. Upper corolla lobes of two populations of *Downingia ornatissima* to show range of variation in position. Above: Variation in population 36 (var. *ornatissima*), from Tehama County, California. Below: Variation in population 27 (var. *eximia*), from Stanislaus County, California. Hairs omitted from drawings; first four types of first row of population 36 with one or two scattered hairs on each corolla lobe; all members of population 27 with hairs on corolla lobes. Numerals show number of individuals of each type.

spots (sometimes confluent) which extend onto two nipple-like folds at the mouth of the corolla tube; corolla tube with three deep violet to very pale (in pale-flowered forms) spots or streaks alternating with the nipple-like folds, otherwise unmarked; upper lobes and tube concolorous with lower lip but usually paler (white in the palest forms).

COLLECTIONS GROWN:

27, in vernal pool in grassland, ca. 1 mi. sw. of Knight's Ferry, Stanislaus Co., Calif., *C. E. Wood 7627 & C. T. Mason*, 9 May 1949 (only this species present, most plants in fruit).

28, in dry vernal pool on Route 120 at Stanislaus Co. line, Tuolumne Co., Calif., *C. E. Wood 7628 & C. T. Mason*, 9 May 1949 (only this species present; plants in fruit).

35, in dry vernal pool with *Eryngium* in rolling grassland on Route 99W, ca. 8 mi. s. of Corning, Tehama Co., Calif., *C. E. Wood 7635, L. Constance, R. Holm & L. Bonar*, 20 May 1949 (seeds; only this species present).

36, in dry roadside vernal pools with *Eryngium* and *Lythrum* just n. of Corning, Tehama Co., Calif., *C. E. Wood 7636, L. Constance, R. Holm & L. Bonar*, 20 May 1949 (seeds; only this species present).

41, w. of Sloughhouse, Sacramento Co., Calif., *G. L. Stebbins, Jr.*, 13 May 1950 (seeds).

42, from low spots in grain field, 3 mi. n. of Sheldon, Sacramento Co., Calif., *G. L. Stebbins, Jr.*, 30 May 1950 (seeds).

45, growing 2 mi. e. of Stockton on State Highway 4, *R. C. Bacigalupi*, San Joaquin Co.,, Calif., 21 April 1951 (seeds).

48, on Hornitos Road, 2.5 mi. s. of Merced Falls, Merced Co., Calif., *R. C. Bacigalupi*, 22 April 1951 (seeds).

INTERSPECIFIC CROSSES ATTEMPTED:

27, 28, 35, 36 × *D. concolor* (34, 87): 129 seeds from 35 capsules (43 from 1 capsule, 23 from another), 14 white lethals, 52 nonhybrids; reciprocal (34, 87 × 27, 35, 36, 42), 47 seeds from 28 capsules, 1 white lethal, 25 non-hybrids.

27, 28, 36 × *D. bicornuta* var. *bicornuta* (30): 235 seeds from 20 capsules, 15 white lethals, 62 nonhybrids; reciprocal (with 28, 36), 14 seeds from 6 capsules, 2 white lethals, 6 nonhybrids.

27, 28, 36, 42 × *D. bicornuta* var. *picta* (40): 214 seeds from 25 capsules, 7 white lethals, 35 nonhybrids; reciprocal (with 28, 42), 26 seeds from 5 capsules, no hybrids, 10 nonhybrids.

27, 28, 35, 36 × *D. cuspidata* (31, 33): 27 seeds from 41 capsules, no hybrids, 10 nonhybrids; reciprocal (with 27, 35, 36), 536 seeds from 33 capsules, 136 white lethals, 78 nonhybrids (note especially 31 × 27: 293 seeds from 6 capsules, 112 white lethals, 48 nonhybrids).

27, 28, 36 × *D. pulchella* (26): 45 seeds from 23 capsules, 2 white lethals (27 × 26), 30 nonhybrids; reciprocal (with 27, 35, 36), 30 seeds from 18 capsules, no hybrids, 28 nonhybrids.

27, 28, 36 × *D. insignis* (14): 35 seeds from 22 capsules, 2 white lethals, 1 greenish yellow, 26 nonhybrids; reciprocal (with 27, 35, 36), 75 seeds from 28 capsules, no hybrids, 65 nonhybrids.

28, 36 × D. *elegans* var. *brachypetala* (39): 80 seeds from 16 capsules, no hybrids, 43 nonhybrids; reciprocal (with 36, 42), 11 seeds from 6 capsules, 1 nonhybrid.

CHROMOSOMES: $n = 12$ in populations 28 (diakinesis) and 42 (metaphase I, metaphase II), the divisions apparently regular. In population 35 no unequivocal count was obtained, but one slide showed two cells at anaphase I with a chromosomal bridge, in one with an accompanying fragment.

Seeds planted in February germinated promptly; the plants flowered in 54–59 days in 1950, 50–52 days in 1951, 51–55 days in 1953. The first flower bud appeared in the axil of the seventh leaf above the cotyledons. In population 35, two counts of 900 grains showed 99.3 and 99.5 per cent stainable grains, and a count of 1000 grains from a plant of population 28 showed 99.4 per cent stainable grains.

Capsules of this species are very tough and apparently indehiscent. In Tehama County, California, in late May, 1949, the shiny, spindle-shaped seeds were being released and scattered by grasshoppers feasting upon the dry, erect capsules of dead plants which carpeted the bottom of a dried-up vernal pool.

Downingia ornatissima is not to be confused with any other member of the genus. As McVaugh pointed out (1941, p. 26), it is readily recognized

by the small projection at the base of the sinus between the two upper corolla lobes, by the corolla tube sparsely hairy within, by the filament tube which is slightly curved backward and which is longer than the dorsal side of the corolla tube, by the anther tube at an angle to the filament tube, and by the bulbous-tipped hairs on the back of the anthers. It is also unique (for the present, at least) in its chromosome number (12).

The species varies from a plant of the northern part of the Central Valley in which the flowers are pale and small and the upper corolla lobes glabrous within and the tip of each often curled backward into a ring, to one at the south of the range in which the flowers are bright (violet to blue) and larger, and the upper lobes divergent and pubescent within near the tips. (See *figs. 4, 5.*) The two extremes were treated as vars. *ornatissima* and *eximia* by McVaugh, who regarded them as "rather formal varieties, and arbitrarily separated as such." He further realized that "as a result of such arbitrary segregation, a single collection will sometimes contain plants of both varieties" and found "this to be true to the greatest degree in collections from Merced and Stanislaus Counties."

In the three collections of var. *eximia* (27, 28, 48, from Stanislaus, Tuolumne, and Merced counties) studied here, all of the individuals had the upper corolla lobes pubescent, but showed much variation in the divergence or curling of the lobes; the flowers were relatively large and intensely colored (deep blue to violet). Those representing var. *ornatissima* (35, 36, from Tehama County), were paler, smaller-flowered (many with the blue restricted to the tips of the corolla lobes), and in nearly all the upper corolla lobes were glabrous (a few with scattered hairs) and with the lobes curled backward in a ring, although some were merely divergent. Collections from the center of the range (*e.g.*, 41, 42 from Sacramento County) were intermediate in flower-size and -color, with the upper lobes divergent or curled, and glabrous or with a few hairs. In a cross between the northern and southern plants (36 × 28), 335 seeds were obtained from 8 capsules (19–75 per capsule). Only about 130 germinated (perhaps due to the two-year lapse between maturity of seeds and planting), but these were green and vigorous with flowers of intermediate color and size. A clinal situation would appear to be present, but this matter should be pursued, particularly in connection with the possibility of incipient genetic barriers within the species. Taxonomically, however, McVaugh's original conclusion seems to hold, the two geographical varieties being only arbitrarily separable.

Downingia pulchella (Lindley) Torrey

FLOWER MORPHOLOGY AND COLOR: See *figs, 6, 7* for conformation and general color pattern of corolla; note divergent upper lobes (with an angle of 85–120° between them) and the nearly plane lower lip; see also Mc-

Vaugh (1941, p. 37), Mason (1957, p. 750). Corolla bright, deep blue (sometimes violet-blue, pink, or white, the last with all anthocyanin suppressed), the lower lip with a central white area; white area with two roughly triangular or wedge-shaped yellow spots, each covering a low, mound-like fold at the base of the lip (the apex at the mouth of the corolla tube) and with 3 dark-purple spots alternating with the folds; purple spots sometimes confluent across the folds, forming a band and interrupting the yellow area; yellow spots sometimes diffuse, the entire central white area being covered; corolla tube narrowly funnel-shaped, dark reddish purple within (purple without), except for a small white area on the lower side at the mouth. See also below for an exceptional variant.

COLLECTIONS GROWN:

25, from wet, muddy soil, Yolo By-pass, e. of Davis, Yolo Co., Calif., *M. Nobs*, May 1949 (in flower).

26, in heavy, gray, mucky clay around borders of a small pool on Route 50 ca. 2 mi. e. of Dublin, Alameda Co., Calif., *C. E. Wood 7626 & C. T. Mason*, 9 May 1949 (plants very abundant, all in flower).

INTERSPECIFIC CROSSES ATTEMPTED:

25, 26 × *D. concolor* var. *concolor* (15, 34, 87), 86 seeds from 16 capsules, 1 white lethal, 67 nonhybrids; reciprocal (with 15, 20, 34, 87), 27 seeds from 18 capsules, no hybrids, 17 nonhybrids.

26 × *D. ornatissima* (27, 35, 36); 30 seeds from 18 capsules, no hybrids, 28 nonhybrids; reciprocal (with 27, 28, 36), 45 seeds from 23 capsules, 2 white lethals (27 × 26), 30 nonhybrids.

26 × *D. bicornuta* var. *bicornuta* (30): 21 seeds from 10 capsules, no hybrids, 29 nonhybrids; reciprocal, 49 seeds from 5 capsules, no hybrids, 38 nonhybrids.

26 × *D. cuspidata* (29, 31, 33): 85 seeds from 37 capsules, 1 white and 9 very pale green lethals, 62 nonhybrids; reciprocal (with 31, 33), 117 seeds from 20 capsules, 5 white or pale green lethals, 33 nonhybrids.

26 × *D. insignis* (14) and reciprocal: See below. Abundant seed set, hybrids very pale green, weak, slow-growing, many inviable, others flowering and fertile; F_2 partially lethal, backcrosses to either parent vigorous and fertile.

26 × *D. elegans* var. *brachypetala* (39): 37 seeds from 10 capsules, no hybrids, 14 nonhybrids; reciprocal, 38 seeds from 9 capsules, no hybrids, 20 nonhybrids.

CHROMOSOMES: $n = 11$ (metaphase II) in population 26; meiosis regular.

Seeds planted in February developed rapidly, the plants flowering in 46–54 days in 1950, and 46–51 days in 1951. Pollen counts showed 90.9 to 99.6 per cent stainable pollen. (See TABLE I.)

With its showy and distinctive corollas 1.5 cm. across and its characteristically exserted filament tube and tapered anther tube, *Downingia pulchella* is not to be confused with any other member of the genus. On morphological bases, McVaugh thought *D. pulchella* to be most closely related to *D. insignis*, a conclusion which is borne out on the basis of chromosomal and genetic data, the two producing weak but fertile hybrids.

Also of this relationship is *Downingia laeta* (Greene) Greene, which ranges from northeastern California, western and central Nevada, and Utah, north to southern Saskatchewan, Montana, southern British Columbia, and western Oregon, to the north and east of *D. pulchella* and *D. insignis*, both of which are primarily Californian. This small-and-pale-flowered species has an androecium and a general corolla pattern most reminiscent of *D. pulchella* and suggestive of derivation from a similar type.

FIG. 6. Variants of *Downingia pulchella*. Upper row: left, the common blue-flowered form referred to in text as "wild type"; right, form with pink corolla lobes. Lower row: left, a small, dark-flowered form; right, form with white flowers, all anthocyanin suppressed; center, a white, small-flowered form from the F_2 of a cross between the two preceding. Flowers seen from above, stamens removed.

An unusual small-flowered mutant form of *Downingia pulchella* which was found in Alameda County, California (see population 26) is of interest in connection with the development of corolla forms and color patterns in the genus. The colony consisted of thousands of densely packed plants, the entire ground appearing to be carpeted with the flowers. Most of the plants bore flowers of the usual blue type described above, but with considerable variation in flower size and in the development of the three spots on the lower lip. Scattered patches of violet, pink, very pale blue, and white plants occurred, with a very few in which the blue anthocyanin was restricted to the tips of the corolla lobes, and at least four in which the white area of the lower lip was strongly suffused with yellow. In addition to these, there were two areas of scattered plants in which the

corollas were small (ca. 1 cm. across) and the lower lip much reduced, all five corolla lobes appearing to be of approximately equal size. (See fig. 6.) The corolla was blue, the white central area was completely lacking, a deep violet area extended from the sinuses between the three lobes toward the base of the lip, and the two yellow areas at the mouth of the corolla tube were restricted as shown in the photograph. On the basis of the corolla alone, these plants were so aberrant that one would hardly suspect that they represented *D. pulchella*; yet it was the only species present in this locality and the stamens were the characteristic ones of *D. pulchella*.

A few simple intraspecific crosses were made later with one of these small, dark "mutants" transplanted from the wild. When crossed with a "wild-type" blue-flowered plant (from population 25 to avoid the possibility of heterozygosity), all of the F_1 plants were of the wild type in respect to both color pattern and corolla conformation. An F_2 obtained by selfing one of these plants was composed of 66 of the wild type and 25 of the mutant type. The small, dark mutant crossed onto one of the white-flowered plants from the same colony also produced an F_1 with flowers of the wild type. The F_2 of 84 individuals from a capsule pollinated from the same plant included 47 of the wild type, 17 white, 16 of the small dark mutant, and 4 of a plant with small white flowers (see lower center, *fig. 6*). The expected results from a cross involving two recessive genes would be in the ratio of 47: 16: 16: 5 for a progeny of 84 plants. The two forms thus segregate independently, and the small, dark mutant behaves as though controlled by a single recessive gene which changes both corolla shape and color pattern. As to whether a gene mutation or some larger chromosomal change or rearrangement is represented, I would not guess, especially since the cytology of these plants was not studied.

So different is the corolla size, the form of the lower lip, and the color pattern, however, that the question arises as to whether a "mutation" of this kind (whatever its nature) might not lead to differential selection by the insect pollinators of this group in which the corolla conformation and color pattern and the anther position are so highly specific.

The general conformation of the corolla is suggestive of *Downingia laeta* (see McVaugh, 1941, *figs. 8, 9*; Mason, 1957, *fig. 340*) and, in fact, of *D. pusilla*, the other species with reduced flowers. The color pattern of the former is quite different, but that of the latter is very similar to the pattern of the double recessive obtained above. One is tempted to postulate the derivation of *D. laeta* from a plant similar to *D. pulchella* and of *D. pusilla* from a plant similar to *D. cuspidata* through changes of this kind.

Downingia pusilla (G. Don) Torrey

FLOWER MORPHOLOGY AND COLOR: See McVaugh (1941, p. 35), Mason (1957, p. 761). Sepals 4–5 mm. long. Corolla limb 4–5 mm. across, the lobes divergent from the tube, the upper and lower lips in about the same plane; lower lip much reduced, the lobes 1.5–2 mm. long, the sinuses extending almost to the mouth of the corolla tube; upper corolla lobes parallel or spreading, about equalling the lower; corolla tube narrow, ca. 2 mm. long; corolla white, unmarked except for a yellow spot at the sinus on either side of the lowermost lobe, the two spots confluent across the lobe at the mouth of the tube.

COLLECTION GROWN: 2063, from 5 mi. n. of Snelling, Merced Co., *R. F. Hoover 2063*, 4 May 1937 (GH) (fruit).

INTERSPECIFIC CROSSES ATTEMPTED:

2063 × *D. concolor* var. *concolor* (34): not attempted; reciprocal, 71 seeds from 2 capsules, 48 weak and nearly white lethals, some surviving almost 4 weeks.

2063 × *D. cuspidata* (29, 31): stigmas protruding from anther tube, flowers not emasculated, 61 seeds from 5 capsules, no hybrids, 47 nonhybrids, 2 capsules each with 25 flat and twisted seeds which aborted near maturity; reciprocal (with 31), 39 seeds from 2 capsules, no hybrids, 20 nonhybrids.

CHROMOSOMES: $n = 11$ (metaphase I, $2n = 11$ bivalents). The plants and buds were so small at the time of meiosis that only a single bud in which only one clear cell was countable was found.

The adaptation of this diminutive species to a fleetingly moist habitat is reflected in the longevity of its seeds and the rapidity of its development. Seeds from *Hoover 2063* in the Gray Herbarium germinated readily fourteen years after collection. Flower buds were visible in 21–28 days when the plants were only 1–1.5 cm. high; meiosis occurred in 26–30 days; and the plants began to flower in 39 days in 1951 or 36 days in 1953. At time of flowering the plants were approximately 4 cm. tall, and most of the photosynthetic area of the plant resided in the ovaries and sepals.

Downingia pusilla appears to be self-pollinated, for the most part, all plants in culture setting abundant seeds, in contrast to other species. Some stigmas protrude, but many expand within the anther tube. Although the possibility of pseudogamy has not been ruled out, other types of apomixis appear unlikely, for when the flower was emasculated or the stigma removed completely seeds were not set. Relatively little pollen was produced by these tiny flowers, and it was difficult either to obtain sufficient amounts for hybridization experiments or to remove the anther tube from this species.

The few crosses attempted with other species are inconclusive, but the chromosome number, the corolla, and the spirally marked seeds all seem to corroborate the relationship of *D. pusilla* to *D. cuspidata* postulated by

McVaugh. *Downingia pusilla*, the most reduced species of the genus, represents one of the end points in the evolution of the group, though one attained without change in chromosome number.

Mason (1957, p. 761) has suggested the possibility of two races of this species, noting that plants from north of San Francisco Bay have white flowers and a corolla tube longer than the lobes, while plants of the Central Valley have blue corollas, a tube shorter than the lobes, and the lower lip conspicuously spreading and often with a distinct palate. *Hoover 2063* should belong with the latter group, but it had, however, no trace of blue in the flowers; the tube and corolla lobes appeared to be approximately equal.

DOWNINGIA INSIGNIS × PULCHELLA,
A WEAK BUT FERTILE HYBRID

Crosses were made between *Downingia insignis* and *D. pulchella* in 1949 and in 1951. Seed-set ranged from about 30 to 100 per capsule and germination rates from 14 per cent in one of the least successful combinations to about 88 per cent in the most successful.

Seedlings were albino to pale yellowish green. Many died in varying lengths of time, but some grew slowly. Those surviving to the time of initiation of flower buds became more vigorous, the ovaries and sepals being green in all instances, presumably adding substantially to the photosynthetic efficiency of the hybrids. From 82 to 108 or more than 118 days (the longest period for which records were kept) were required from time of planting to time of production of the first flowers.

The various crosses between the two species are summarized below.

Downingia insignis × *pulchella* (F_1):

92 (14 × dark, small-flowered mutant of 26): ca. 125 seeds from 2 capsules, ca. 65–75 pale green hybrid seedlings, about 40 surviving six weeks, one producing a very small and pale flower in 100 days, this and other plants later succumbing to attacks of white flies and mites.

95 (14 × white 26): ca. 50 seeds from 1 capsule, 44 pale green seedlings, 37 surviving at time of first flower (82 days after planting), 20 plants surviving to flower. (See below.)

96 (14 × 25): ca. 90 seeds from 1 capsule, 8 hybrid seedlings all pale and spindly, none surviving more than 40 days.

99 (14 × 25): ca. 80 seeds from 1 capsule, 17 very pale and weak hybrids, none reaching flowering, 1 nonhybrid.

100 (14 × pink 26): ca. 35 seeds from 1 capsule, 7 very pale green hybrids, no survivals.

153 (14 × 26): 50 seeds sown, 38 hybrids, 1 nonhybrid; all hybrids pale green and weak: 3 lasting 65 days, 1 almost reaching flowering (108 days), but succumbing to an attack of *Botrytis*.

157 (14 × 26): 104 seeds (of ca. 335 from 2 capsules) sown, 70 per cent germinated; 64 white or pale green hybrids, 9 nonhybrids; 4 hybrids still alive after 118 days with buds but as yet no flowers.

Downingia pulchella × *insignis* (F₁):

93 (26 white × 14): 75 seeds from 1 capsule; 11 very pale and spindly hybrids, only one surviving to flower; 1 nonhybrid [white-flowered *D. pulchella*].

94 (26 white × 14): ca. 75 seeds from 1 capsule; 22 pale and spindly hybrids, none of which survived more than 50 days, nor flowered; 2 nonhybrids (white-flowered), in 56 days.

98 (25 × 14): ca. 100 seeds from 1 capsule; ca. 25 pale and spindly hybrids, none of which survived to flower; 4 nonhybrids (blue-flowered, one with 3 spots at base of lip confluent in a band).

101 (25 × 14): ca. 200 seeds from 2 capsules; ca. 75 spindly, pale green seedlings, most dead within 50 days (one surviving to flower); 6 nonhybrids (the first flowers in 48 days).

154 (26 × 14): 100 seeds sown; 58 pale hybrids, none surviving more than 63 days, none flowering.
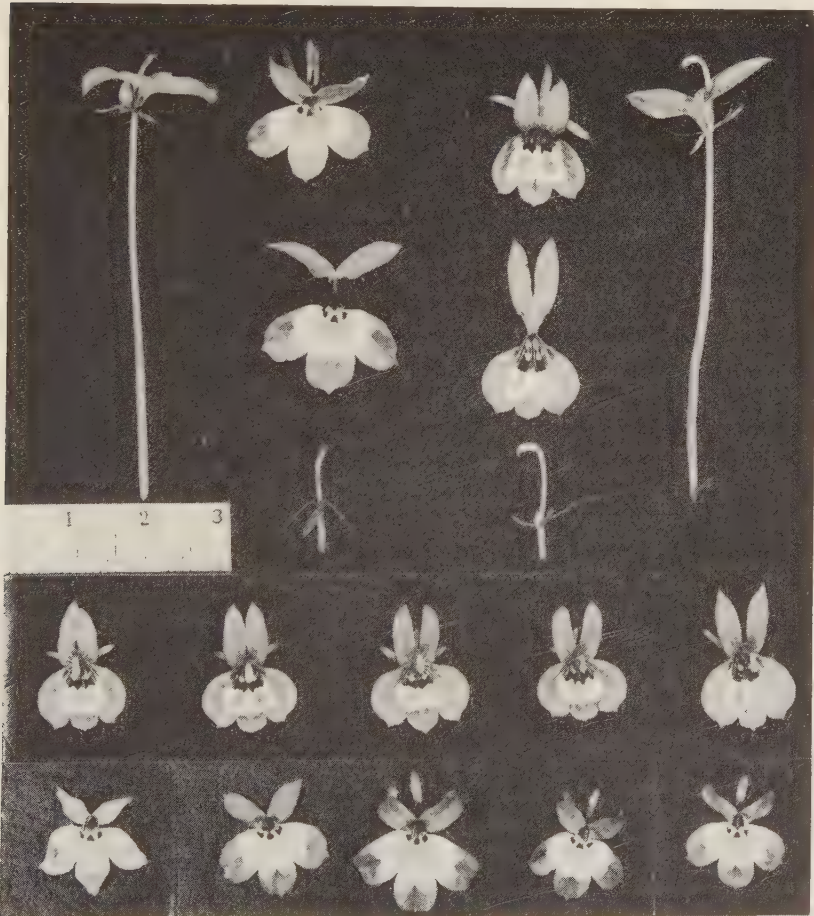

Fig. 7. Flowers of *Downingia pulchella* (above, left, and lower row of five flowers) and of *D. insignis* (above, right, and upper row of five flowers).
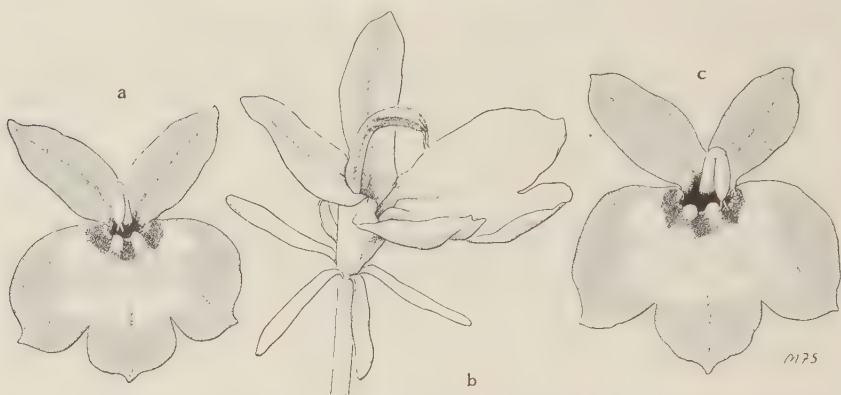
Fig. 8. Flowers of first-generation hybrid (population 95) of *Downingia pulchella* and *D. insignis*: a, c, flowers of two plants to show form and color pattern of corolla; b, flower with markings omitted, to show androecium and conformation of upper and lower lips. Compare with *figs. 1m, s* and 7.

155 (26 × 14): 29 seeds from 1 capsule: 24 pale green hybrids, 6 surviving 70 days, but none surviving to flower (a heavy growth of *Vaucheria* on the soil surface perhaps partly responsible).

156 (25 × 14): 100 seeds planted; 52 pale yellowish-green hybrids; 1 nonhybrid (removed); 5 hybrids (all pale and spindly) surviving to flower after 103 days.

Population 95, a cross between the blue-flowered *Downingia insignis* and a white-flowered plant of *D. pulchella*, was the most successful of the hybrids. In this population, sown 17 February 1950, germination was 88 per cent, proceeding over a three-week period. The seedlings were all pale yellowish green and very slender and grew slowly, the largest being only 1.3 cm. tall after seven weeks. When the first flowers opened, 82 days after sowing, 37 plants from 0.4 to 14 cm. tall still survived. Twenty plants lived to flower by May 20. The stems of all of these remained very pale green, reddish near the base. The leaves produced up to the time of flower-bud initiation were pale, but those with axillary flower buds were bright green, and the ovaries of all flowers were green.

The two parental species differ in a whole series of floral characteristics, many of which will be immediately apparent from an inspection of *fig. 7*. Among those of the corolla are the shape, length, and diameter of the tube; the form and concavity of the lower lip and its angle to the corolla tube; the angle between the upper lobes and their angle to the tube; and the markings of the lower lip and the corolla tube. Features of the androecium include the length of the filament tube; the length, shape, and color of the anther tube and its angle to the filament tube; and the length and shape of the hairs on the anther tube.

The flowers of the F_1 hybrids were intermediate in most respects (see *fig. 8*), in shape more suggestive of *Downingia insignis* but with a much

narrower corolla throat, a somewhat flatter lower lip and more divergent upper lobes. The color pattern was also intermediate: the white area had the general form of that of *D. pulchella*, but showed the restriction evident in *D. insignis*, and the three dark spots at the base of the lip varied from separate, but larger than usual in *D. pulchella*, to more or less confluent in a narrow band across the two low yellow folds, undoubtedly reflecting the heterozygosity of the parental plants. (Self-pollination of wild plants of *D. pulchella* produces offspring with considerable variation in the shape of the corolla and in the spotting of the lip, sometimes with much larger spots and these sometimes confluent across the low ridges as above.) The

TABLE I. Pollen Fertility in Downingia insignis, D. pulchella, and Hybrids

POPULATION	TOTAL GRAINS COUNTED	PER CENT STAINABLE POLLEN	PER CENT ABORTED POLLEN
D. insignis			
14	1600	94.0	6.0
14	2100	99.4	0.6
14	1800	98.9	1.1
14	1500	98.3	1.7
14	1800	99.4	0.6
14	2000	99.7	0.3
D. pulchella			
26	2000	99.6	0.4
26, white, selfed	1200	90.9	9.1
25	1600	98.0	2.0
25	1600	98.1	1.9
D. insignis × *pulchella* (F_1)			
95	1100	94.2	5.8
95	1500	93.7	6.3
95	1800	98.8	1.2
95	850	94.6	5.4
D. pulchella × *insignis* (F_1)			
93	975	95.2	4.8
93	930	92.9	7.1
101	1350	95.8	4.2 [a]
D. insignis × *pulchella* (F_2)			
203 (95 × 95)	1000	98.7	1.3
203	1100	95.4	4.6 [b]
203	1200	90.8	9.2 [c]
203	1000	97.2	2.8 [d]
203	1100	99.1	0.9

[a] Including three giant grains, and many grains slightly smaller than usual; greater variation in pollen size than usual.

[b] Considerable variation in size; pollen grains appearing much below normal counted as aborted although contents present.

[c] No size variation; all grains clearly aborted.

[d] Considerable variation in size, including grains larger and smaller than normal.

androecium is also intermediate: the filament tube in length and the anther tube in shape, angle to the filament tube, and marking (slightly darker than the dirty white anthers of *D. insignis* but lighter and less pronouncedly blue-gray striped than in *D. pulchella*). The hairs on the anther tube were slender and intermediate between the short, stubby hairs of *D. insignis* and the relatively long, slender ones of *D. pulchella*. Aside from the variation in the dark spots at the base of the lower lip, the flowers of the twenty plants of this population were remarkably uniform. Although the flowers generally were somewhat smaller in size than those of either parent, this, as in many annuals, was related to the vigor of the plant rather than to other factors, the most vigorous of the hybrids also bearing the largest flowers. The ovaries ranged from 2.5 to 3 cm. in length and the capsules from 2.5 to 3.7 cm.

Chromosome counts were not attempted on the hybrids because of the small number of surviving plants and their general lack of vigor. Pollen counts, however, showed a range of pollen stainability (and presumably fertility) of 92.9 to 98.8 per cent, approximately the same as that of the parental species. (See TABLE I.) Seed set by the hybrids and in backcrosses bore out this supposition of fertility. However, the pollen variations seen in the surviving plant of population 101 suggest at least a low frequency of meiotic irregularities.

Backcrosses. A number of backcrosses from populations 93 (a single surviving plant) and 95 were made to each of the parents. The hybrid was used as the pollen parent in all except a single instance because of the general weakness of the hybrid plants and the desirability of using the relatively few flowers for the production of a second hybrid generation. The results are summarized below:

BACKCROSSES OF F_1 TO *Downingia pulchella*:

205 (26 white $\times$ 95): 85 seeds from one capsule, 77 green seedlings, 1 albino lethal; all greens vigorous, the first flowers in 52 days.

206 (95 $\times$ 26 white): ca. 75 brown seeds plus an approximately equal number of nearly white seeds from 1 capsule; ca. 95 germinated, ca. 63 white or pale lethals, 22 pale and weaker, 10 vigorous and green which flowered after 52 days. (Possible contamination with F_1 pollen? Cf. F_2 below.)

207 (26 $\times$ 95): 260 seeds from 3 capsules, 1 albino lethal, 210 green and vigorous, the first flowers in 47 days.

208 (26 $\times$ 95): 70 seeds from 1 capsule, 65 green and vigorous seedlings, the first flowers in 45 days.

209 (26 $\times$ 95): 100 seeds from 1 capsule, good germination (number not recorded), all seedlings green and vigorous, the first flowers in 45 days.

210 (25 $\times$ 93): 100 seeds from 1 capsule, 1 white lethal, numerous green and vigorous seedlings (not counted), the first flowers in 47 days.

BACKCROSSES OF F_1 TO *D. insignis*:

211 (14 $\times$ 93): 157 seeds from 2 capsules, 1 white lethal, numerous green and vigorous seedlings (not counted), first flowers in 47 days.

212 (14 $\times$ 95): 649 seeds from 9 capsules (ca. ½ sown), 1 pale lethal, numerous green and vigorous seedlings (not counted), the first flowers in 47 days.

213 (14 × 95): ca. 120 seeds from 1 capsule, numerous green and vigorous seedlings, the first flowers in 50 days.

With the exception of the possibly contaminated cross (206) in which the hybrid was used as the seed parent, in each of the combinations above the seed-set and excellent germination indicate full fertility and vigor. The seedlings were green and vigorous, grew rapidly, and flowered in 47–52 days, the period required for the parental species. As would be expected, the variation ranged roughly from the F_1 to the backcross parent. Populations obtained from backcrosses in each direction are shown in *figs. 9* and *10*.

Only one plant of population 209 was examined cytologically. Numerous divisions at anaphase I and metaphase II were seen. All divisions appeared to be regular, except for two cells at anaphase I showing traces of a lagging chromosome or bridge and one at metaphase II with one plate of eleven chromosomes, the other of eleven plus a fragment.

The Second Generation. Various combinations of the single survivor in population 93 (*Downingia pulchella* × *insignis*) and those in 95 (*D. insignis* × *pulchella*) were tried in 1950. The results are summarized below:

Downingia insignis × *pulchella* (F_2):

200 (93 selfed): 181 seeds from 3 capsules from a single plant, 59 white or pale green lethals, 117 varying from weak and pale, to vigorous and green, most plants green eventually but some definitely more vigorous than others; first flowers in 52 days.

201 (93 × 95): 142 seeds from 2 capsules (with 12 and 130 seeds), 110 seeds germinating, 55 white or very pale lethals, 55 pale green, yellowish-green, or green seedlings showing great variation in vigor, 0.9–6.5 cm. tall after 42 days; first flowers in 50 days.

202 (95 × 93): 2 seeds from each of 2 capsules, 1 white lethal, 1 pale green (died in 30 days), 2 slow-growing pale greens flowering after 60 days.

203 (95 × 95): 454 seeds from 8 capsules, 114 white or pale green lethals, 85 yellowish-green to green survivors with much variation in vigor (0.5–4.4 cm. tall after 42 days), first flowers after 52 days.

204 (95 selfed): 68 seeds from one capsule, 31 white or pale lethals, 23 of various shades of green surviving, with wide range of vigor (0.6 to 1.8 cm. tall after 42 days), no record of flowering.

Seed set averaged 50 to 70 (extremes 2–130) per capsule and germination was generally excellent. Thirty to fifty per cent of the F_2 seedlings were albino or pale green lethals, while the remainder ranged from pale green to vigorous, bright green plants, many of which survived to maturity. In contrast to the F_1 generation, flowering began in about 52 days (approximately the same period required for the flowering of the parents). Pollen stainability (see TABLE I) ranged from 91 to 99 per cent in five plants of population 203.

Obviously many segregant combinations were eliminated in the F_2. As

Fig. 9. Flowers of thirty plants of a backcross, population 211: *Downingia insignis* (14) × (*D. pulchella* × *insignis*, population 93). Natural size.

will be seen from *figs. 11* and *12* which illustrate individuals of populations 200 and 203, the recombinations in no instance duplicate the parental types exactly, and most resemble the F₁. Although the *Downingia pulchella* parent in the original crosses was white-flowered, the few white-flowered

FIG. 10. Flowers of thirty plants of a backcross, population 207: *Downingia pulchella* (26) $\times$ (*D. insignis* $\times$ *pulchella*, population 95). Natural size.

segregants in the F_2 were more like *D. insignis*, although with divergent corolla lobes. In one bizarre individual of this population the corolla and androecium were suppressed altogether, but the stigma was well developed, and apparent stigmatic surfaces were found on the tip of each of the sepals.
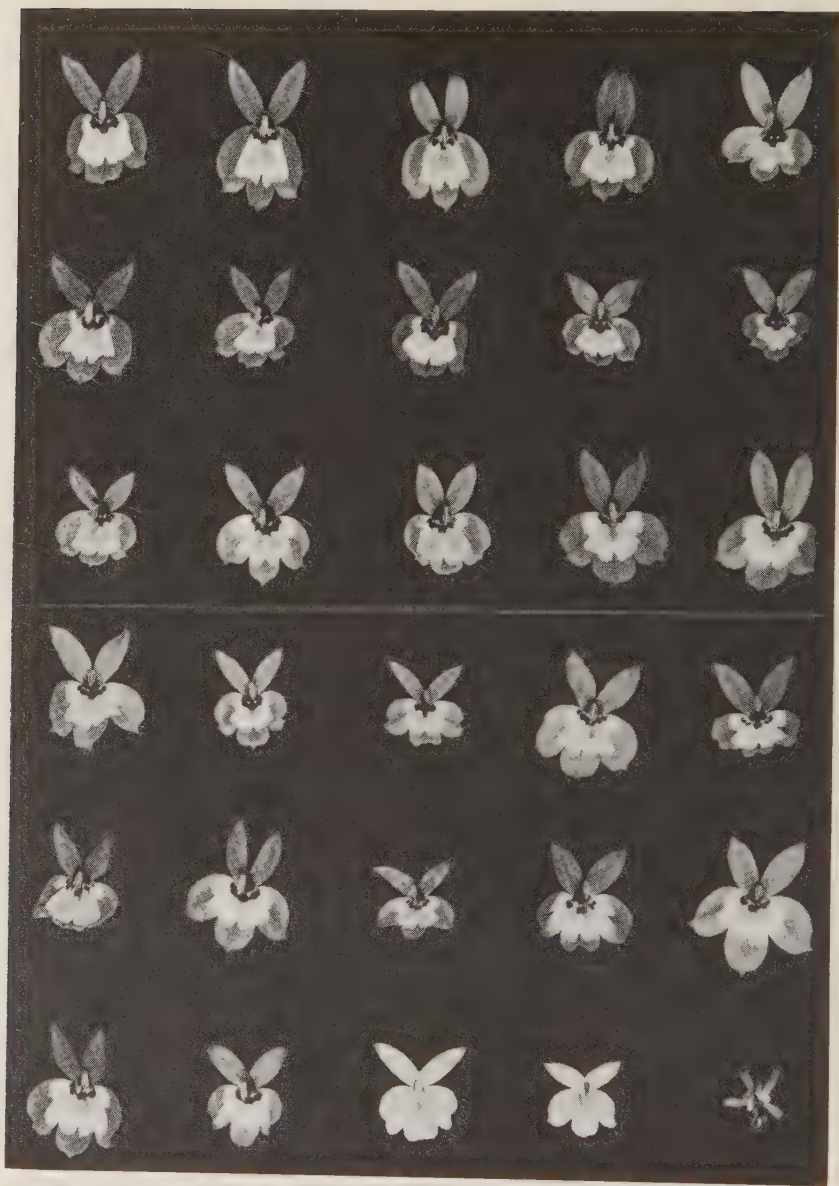
Fig. 11. Flowers of thirty plants of second-generation hybrid of *Downingia pulchella* × *insignis*: population 200 from self-pollination of the single survivor of F₁ population 93. Plant at right in bottom row lacked corolla and stamens and had apparent stigmatic lobes on tips of sepals. Natural size.
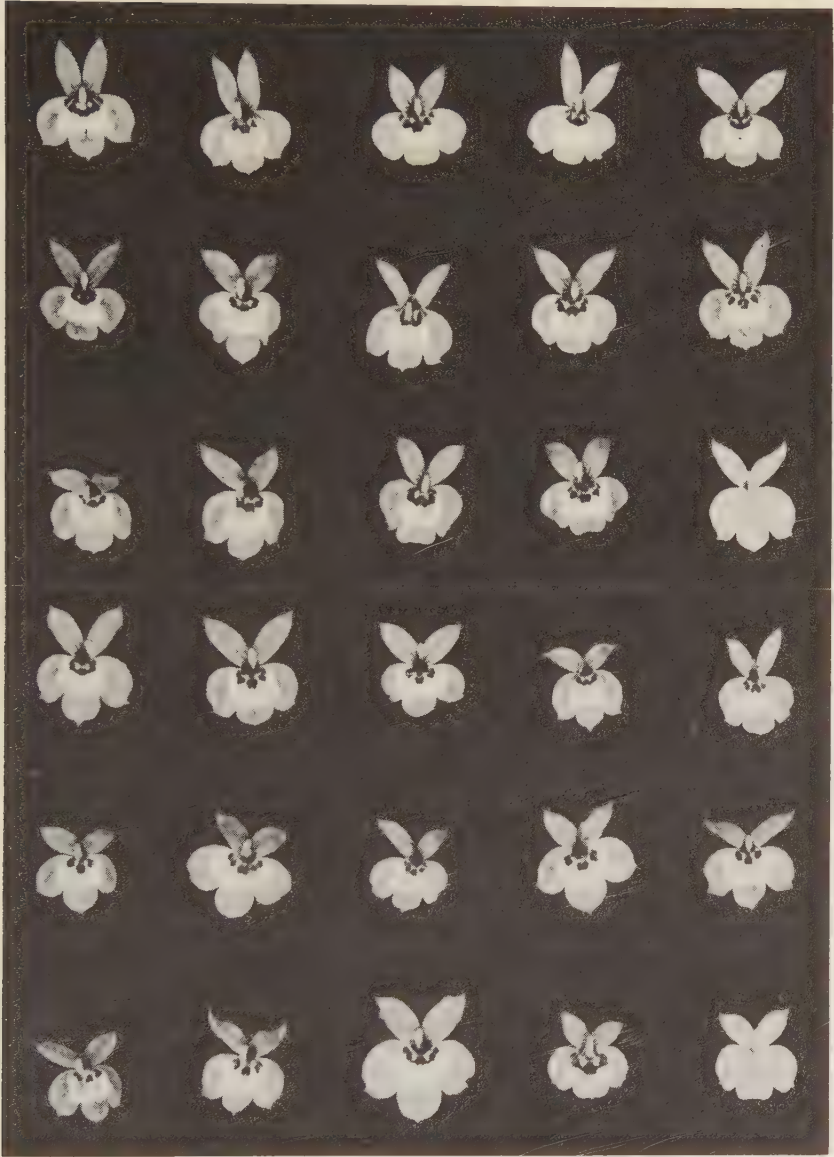
FIG. 12. Flowers of thirty plants of second-generation hybrid of *Downingia insignis* × *pulchella*: population 203 from 95 × 95. The *D. pulchella* parent in this and in *fig. 11* was a white-flowered form. Natural size.

The Third Generation. Most of an F_3 generation was lost at Chapel Hill in 1952, a year in which all seeds sown failed. In 1953, four sowings, each derived from a single capsule and involving a cross within population 200, the F_2 of 93 (*D. pulchella* $\times$ *insignis*), were made. Seeds ranged from sixteen to sixty per capsule, but only two to fifteen per capsule germinated, perhaps in part because of the two-year delay in planting. Seedlings were yellow to moderately green, but none was very vigorous. All grew very slowly, and none survived to flower.

From the above data it is evident that hybrids between *Downingia insignis* and *D. pulchella*, both of which have 11 pairs of chromosomes, are easily produced artificially and that germination of hybrid seeds is good. The interaction of the two gene complements produces physiological diffi-culties, however, and the hybrids are albino or chlorotic, inviable or weak, requiring (when surviving at all) very much longer than the parental species to flower. They are fertile, however, setting abundant seed with other hybrids or producing green and vigorous offspring in backcrosses. The second generation includes many genetically unbalanced plants, in-cluding a high proportion of albinos and chlorotic plants which do not survive. However, some of this generation are more vigorous than the first and flower in about the same length of time as the parental species. Al-though the data on a third generation are quite inconclusive, physiological weakness seems to continue.

In spite of the weakness of the first generation hybrid, there is the potentiality for gene exchange between the parental species, especially by backcrossing. It seems very unlikely, though, that such ever occurs in the wild populations in which *Downingia insignis* and *D. pulchella* grow to-gether (as they sometimes do). No field data are available, but several factors which may work against any genetic exchange are immediately apparent. Insect pollinators of the two species have not, to my knowledge, been studied. The highly specialized flowers suggest, however, the possi-bility of a barrier to interspecific pollination due to differences in pollinators of the two species, or to differences in the preferences of a single pollinator for a particular color pattern, or to the mechanical barrier of the position of anthers and stigma. Assuming, though, that pollination may occur, the genetic chlorosis of the hybrids and the consequent (?) weakness and slowness of growth would result in the elimination of hybrid plants from wild populations before they could backcross with either parent or mature seeds themselves. The hybrids are either (1) too weak to survive the rigors of the mild winter or of the vernal pool habitat in general, or (2) cannot compete with the parental or other species, or (3) grow so slowly that they are out of synchronization with the drying up of the vernal pools and the flowering of the parental species and may not even be able to flower at all. Any or all are likely.

In the spring of 1951, a number of greenhouse experiments were essayed to test the survival potentialities of hybrids in competition with the parental species. As controls, fifty seeds of each of the parental popula-tions (*D. pulchella* 26, *D. insignis* 14) and of three hybrid crosses (154,
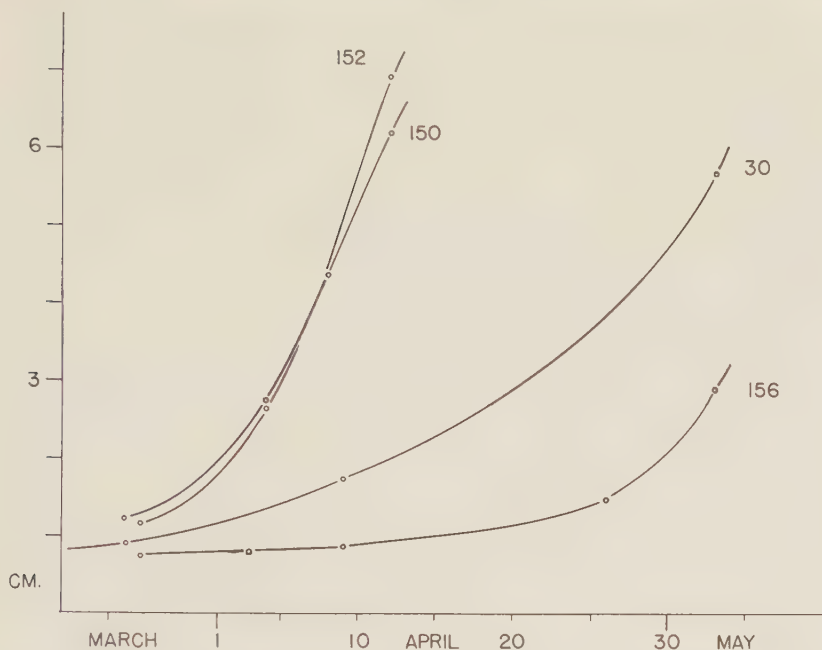
Partial growth-curves of *Downingia insignis* (150), *D. pulchella* (152), their F₁ hybrid (population 156), and the slowest growing of the species, *D. bicornuta* var. *bicornuta* (30). Based on means of heights of varying numbers of plants, graph is intended only to give approximate comparisons of vigor and rapidity of maturation, not statistically accurate growth rates and ranges of variability. Measurements for 150 and 152 were taken respectively from 20 to 36 plants; those for hybrid began with 47 plants but drop to 41, 37, 11, and finally 5 survivors; for *D. bicornuta* involve only two plants grown separately. All seeds sown 28 February 1951; flowering of 150 and 152 began on 12–14 April, of hybrid on 5 June, and of *D. bicornuta* on 6 May.

155, 156; see F₁ above) were planted in 6-inch azalea pots. Ten combinations of hybrid and parental seeds totalling 60 to 300 seeds to each 6-inch pot and in proportions of hybrids to equal numbers of parental seeds of 1:2 to 5:1 were also sown at the same time. Even when grown alone in the controls (see F₁ above), these particular hybrids were hardly successful, and progressed slowly, only five of population 156 surviving to flower after 103 days. In none of the competitions did any hybrids survive to flower, whereas, no matter how crowded the pot, many of the nonhybrids flowered in 45–50 days. Unless combinations of *D. insignis* and *D. pulchella* other than the few tried here produce very much more vigorous hybrids, it seems that a seedling hybrid of these two species stands little chance of survival in the wild.

DISCUSSION

The species of *Downingia* form an aneuploid series with 8, 9, 10, 11, and 12 pairs of chromosomes. Eleven (which occurs in five species) appears

to be the basic number, especially since the less specialized *Porterella carnulosa*, the closest relative of the genus, also has eleven pairs (Carlquist, Madroño 13: 206. 1956).* In addition, both *D. elegans* var. *brachypetala* (10 pairs) and *D. ornatissima* (12 pairs) show morphological specializations indicative of derivation; and the occurrence of eight or nine pairs in different populations of *D. concolor* suggests both specialization and continuation of the aneuploid trend. Hybrids between the two chromosomal races of *D. concolor* should yield evidence from their meiotic behavior of the manner in which aneuploidy has occurred in the genus, and somatic chromosome morphology should provide additional clues.

Chromosome numbers and hybridization data are summarized in *fig. 13*, in which the species have been arranged on the basis of morphological and genetical similarities. The diagram includes reciprocal interspecific crosses in all possible combinations, except some involving *Downingia pusilla* and those between *D. bicornuta* var. *picta* and *D. insignis* and *D. pulchella*, none of which was made.

It is clear from the crossing results that species of *Downingia*, at least as represented by these populations, are well separated genetically, with strong barriers to hybridization. Interspecific crosses fail to produce embryos; the seeds abort near maturity or the hybrid seedlings are albino; or, exceptionally, the hybrids are weak and slow growing but fertile. These categories mark three genetic groups into which the eight species fall.

The first comprises only *Downingia elegans* var. *brachypetala* which stands in complete isolation, for not even partially developed seeds were obtained in any of the hybrid combinations attempted.

A second group, including *Downingia bicornuta*, *D. concolor*, *D. cuspidata*, *D. ornatissima*, and *D. pusilla*, shows very strong interspecific genetic incompatibilities, but the production of more or less numerous albino seedlings in various combinations of these species provides evidence of closer relationships within the group than outside it. The differences found in most reciprocal crosses between these species (e.g., the production of relatively numerous albino seedlings when *D. cuspidata* is used as the seed parent, but the failure to set seeds when this species is the pollen parent) suggest a prefertilization barrier to hybridization, in addition to the strong incompatibilities of the gene complements in the hybrids.

The third includes *Downingia pulchella* and *D. insignis* which are isolated from the other species grown, producing only an occasional albino seedling with some members of the preceding group. The two species are potentially capable of interbreeding, but their hybrids are albino or chlorotic, weak and slow growing. Those surviving to flower, however, are

* McVaugh's earlier report (1943, p. 25) of $n = 12$ for this species (*McVaugh 6282*, Lake County, Oregon) was overlooked when the manuscript was being prepared. Carlquist's count was based on *Mason 14439* (UC), from Sierra County, California. In spite of the apparent aneuploidy in this widespread species ("northwestern Wyoming to southeastern Oregon, south in the mountains to northern Utah, Coconino County, Arizona, northern Nevada, and Tulare County, California"), eleven would still seem to be the basic number in *Downingia*.
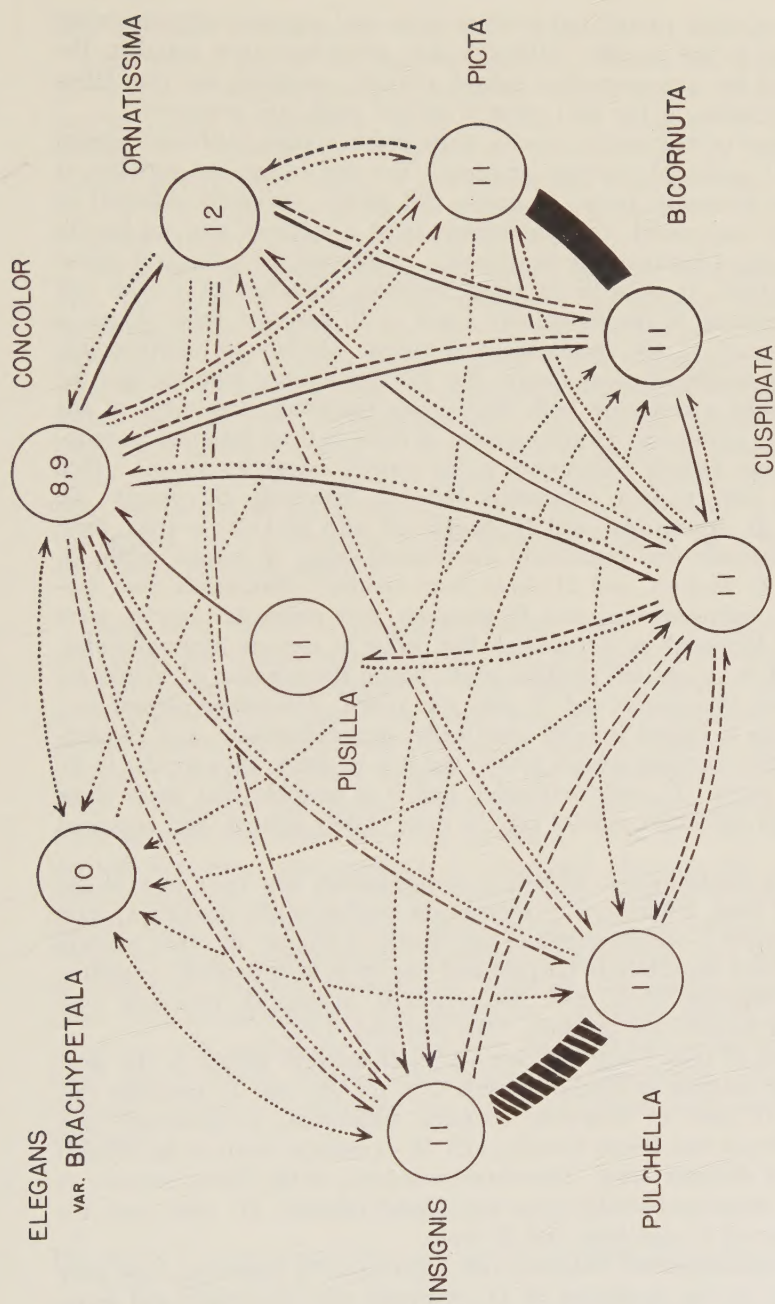
FIG. 13. Crossing relationships and chromosome numbers of eight species of *Downingia*. All crosses attempted are shown. Arrows indicate direction of cross; those unsuccessful in both directions are shown by a single dotted line with arrow at both ends. Dotted line, no trace of hybrid seeds; dashes, production of an occasional albino lethal (averaging less than one per capsule); thin solid line, frequent hybrid lethals; broad striped band, albino or chlorotic but fertile hybrids; broad black band, vigorous fertile hybrids. See text.

as fertile as either parent and produce green and vigorous offspring when backcrossed to the parents. Although they sometimes grow together, the weakness of the first-generation hybrid probably precludes any possibility of gene exchange in the wild, even if hybrid seeds are produced.

In contrast to interspecific crosses, those within species (although limited in number) produced vigorous seedlings. The two recognized varieties of *Downingia bicornuta* (vars. *bicornuta* and *picta*), strikingly different in morphology, geography, and physiology, yield a vigorous and apparently fertile hybrid of intermediate morphology, confirming the taxonomic status accorded them. It is to be expected, however, that further studies will show, in addition to the aneuploidy found in *D. concolor*, other stages in speciation, such as the development of genetic barriers to interbreeding.

Data are lacking for four species, but the chromosome numbers and the genetic results corroborate both McVaugh's taxonomic treatment of the eight species grown and his arrangement of these in three informal morphological groups (which correspond to the genetic categories above). (See McVaugh, 1941, p. 10.) *Downingia bella*, *D. bicornuta*, *D. concolor*, *D. cuspidata*, *D. ornatissima*, and *D. pusilla*, all with bilocular ovaries, form a morphologically and genetically interrelated group of species, while *D. pulchella*, *D. insignis*, and *D. laeta* form another. *Downingia yina* (including *D. willamettensis*) and *D. montana*, with unilocular ovaries, were treated by McVaugh as still another line, while *D. elegans*, also unilocular, was placed in an isolated position, even though the question of hybridization between this species and *D. yina* was raised. *Downingia elegans* var. *brachypetala* is indeed isolated genetically, morphologically, and chromosomally from the other species grown, but it is in many ways similar to *D. yina* var. *major* (*D. willamettensis*), and it is possible that these three species with unilocular ovaries may be more closely related than appeared at first.

Although strong genetic barriers to hybridization now exist, and, in the absence of these, differences in chromosome number might produce at least partial barriers to interbreeding of the species, a number of other barriers may have been important in the past and may be at least partially operative at the subspecific level now. Geographical, ecological, temporal, and mechanical barriers are possible. (See Stebbins, 1950.)

Occurring in both California and Chile, *Downingia pusilla* is the most spectacular example of spatial division of a species; but *D. concolor* var. *concolor*, of Lake to Monterey counties, California, is separated from var. *brevior*, of San Diego County, and *D. cuspidata* seems to be divided into several disjunct areas. *Downingia montana*, of the Sierra Nevada, is separated ecogeographically from its closest relative, *D. yina*, and the same is true of *D. pulchella* and *D. laeta*.

Both ecogeographical isolation and differences in flowering time may play a part in the separation of *D. bicornuta* vars. *bicornuta* and *picta*, which in cultivation flower about two weeks apart. However, subspecific variation in this species is more complex than has been thought and needs further study. *Downingia insignis* and *D. elegans*, perfectly distinct but

long confused taxonomically, also show differences in time of flowering.

Field studies will be necessary to determine whether real ecological differences exist between otherwise sympatric species. Some species do occur together, such combinations as *D. concolor–D. insignis*, *D. elegans–D. insignis*, *D. bicornuta–D. cuspidata–D. concolor*, and *D. pulchella–D. insignis* having been found. Eight species are reported from Stanislaus County, California, but no further information is available as to their distribution within this center of concentration.

Mechanical barriers to crossing are among the most intriguing possibilities. The variation in length and position of the stamens, their peculiar pollen discharge mechanism, and the wide range in size and coloring of the elaborate corollas strongly suggest specific insect pollinators. It does not seem likely, for example, that the same bee which has its face dusted with pollen from the short, included stamens of the modest flowers of *D. concolor* could pollinate nearby *D. insignis* with its large and showy lower lip, broad corolla tube, and strongly exserted stamens. Careful field observations are needed on pollinators and their behavior, not only in respect to the species, but to mutations in the form and color of the corolla. (See *Downingia pulchella* above.)

These eight species of *Downingia* emerge, then, as distinctive, highly specialized semiaquatic winter annuals, well adapted to a transient habitat. A large number of individuals may occur within a small area, but because of the nature of the habitat the populations are discontinuous. Although self-compatible, the plants are adapted for insect pollination and are outcrossing (with the apparent exception of the most reduced species). As a result, individuals are highly heterozygous. The chromosome numbers form an aneuploid series centering around 11, with 8, 9, 10, and 12 as derived numbers. The presence of occasional chromosomal bridges in meiotic divisions and of different chromosome numbers within a single species show that chromosomal repatterning continues within the genus. Poorly to highly differentiated geographical races attest to a whole series of subspecific levels of development. However, the species are well separated, both morphologically and genetically. Although spatial, ecological, temporal, and mechanical barriers may be operative below the specific level, strong genetic barriers exist between species, which, although presumably evolved allopatrically, can now exist sympatrically without gene exchange.

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